Part III: Postcranial skeleton

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ABSTRACT

The earliest and most complete articulated skeletons of fossil metatherians yet known are represented by four specimens of *Pucadelphys andinus* from the Santa Lucía Formation (early Paleocene) at Tiupampa in southcentral Bolivia. Two sets of what are interpreted to be male-female pairs were found in a three dimensional, life-like, snout-rump position in burrow-nests that were apparently dug in a bank along a meandering river. The animals probablydie d as the result of a flood which entrapped them in their burrows and filled the latter with water and sediment. A detailed comparative study of the postcranial bones reveals that the vast majority of character states in *Pucadelphys* are regarded as mammalian, tribosphenic or metatherian plesiomorphies (e.g. atlas not perforated by transverse canal and with a persisting suture between the ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; robust fibula; presence of ossified os marsupium; etc.). Character states of uncertain polarity include the presence of only one vertebra articulating with the ilium (fulcral vertebra), and a long non-prehensile tail. The tarsus has a bicontact upper ankle joint (UAJ) as in living Didelphidae; moreover the calcaneum shows a partially plantar orientation of the cuboid facet which can be interpreted as foreshadowing the specialisation of later Didelphidae; the situation then is more advanced than in the "plesiomorphic metatherian morphotype" of SZALAY (1982 a, b; 1984); the only characters of the latter persisting in *Pucadelphys* are the large peroneal process and the "remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum". Collectively these characters support the view, based on the study of the skull and dentition (MARSHALL & MUIZON, 1995), that *Pucadelphys* represents the plesiomorphic taxon within the family Didelphidae. Functional considerations of the skeletons suggest that *Pucadelphys* was essentially terrestrial, quite agile, and possessed limited bounding and digging capabilities.

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RÉSUMÉ

Troisième partie : le squelette postcrânien

Les squelettes les plus anciens et les plus complets de métathériens fossiles connus à ce jour sont représentés par quatre specimens de *Pucadelphys andinus*, en provenance de la Formation Santa Lucia (Paléocène inférieur), à Tiupampa, dans le sud de la Bolivie centrale. Deux ensembles de ce que nous avons interprété comme des couples mâle-femelle ont été conservés en trois dimensions, en position de vie, et disposés tête-bêche dans ce qui semble avoir été la berge d'un méandre fluviatile. Ces animaux sont apparemment morts à la suite d'une inondation qui les a piégés dans leur terrier en remplissant ce dernier d'eau et de boue. L'étude détaillée et comparée des os postcrâniens a révélé que la grande majorité des caractères de *Pucadelphys* peuvent être considérés comme étant dans un état plésiomorphe pour les Mammifères, les Tribosphenida et/ou les Métathériens (*e.g.* atlas imperforé et gardant une suture entre l'intercentre ossifié et l'arche atlantale ; axis dépourvu de canal transverse, mais possédant une côte libre persistante ; absence de véritable canal transverse sur CV7 ; fibula robuste ; présence d'un os marsupium ossifié ; etc.). L'existence d'une seule vertèbre fulcrale (S1) et d'une longue queue non préhensile constituent, eux, des caractères de polarité incertaine. L'articulation du tarse est de type «bicontact» comme chez les Didelphidae actuels ; en outre la facette cuboïde du calcanéum présente une orientation en partie plantaire qui peut être interprétée comme préfigurant la spécialisation des Didelphidae ultérieurs ; ce tarse est donc plus spécialisé que celui du «plesiomorphic metatherian morphotype» de SZALAY (1982a,b ; 1984), ne le rappelant que par le grand processus péronéen du calcanéum et la largeur remarquable qui sépare ce processus et le bord médial du sustentaculum. Prise dans son ensemble, cette analyse du squelette soutient l'opinion, basée sur l'étude du crâne et de la denture, selon laquelle *Pucadelphys* représente le taxon plésiomorphe à l'intérieur des Didelphidae. Les considérations fonctionnelles résultant de l'étude de ces squelettes suggèrent que *Pucadelphys* était un animal essentiellement terrestre, plutôt vif et capable, dans certaines limites, de sauter aussi bien que de creuser.

RÉSUMÉ DÉVELOPPÉ

Les restes de squelettes postcrâniens des mammifères paléogènes sont extrêmement rares et, qui plus est, difficiles à identifier en raison de l'absence d'association avec les dents, organes sur lesquels est essentiellement fondée la taxonomie de ces animaux.

Or les squelettes étudiés dans cette troisième partie sont non seulement associés à des crânes munis de leur denture (voir Part. II de ce volume), mais ils sont très complets (95% des os sont représentés) et très bien conservés. Ils sont enfin les plus anciens restes squelettiques connus de marsupiaux, cette position étant jusqu'ici tenue par des os tarsiens isolés du Paléocène supérieur d'Itaboraí, Brésil.

L'étude détaillée de ces squelettes est donc du plus haut intérêt. Les comparaisons ont été faites, d'une part avec les rares squelettes connus de mammifères mésozoïques: l'éothérien *Eozostrodon*, du Jurassique inférieur d'Afrique du Sud, le thérien non tribosphénique *Henkelotherium*, du Jurassique supérieur du Portugal, et les placentaires du Crétacé inférieur de Mongolie ; avec d'autre part les petits didelphides généralisés actuels : *Metachirus, Monodelphis, Marmosa* et *Didelphis*, avec aussi *Perameles*.

La colonne cervicale de *Pucadelphys andinus* est celle d'un petit didelphide actuel, si ce n'est que l'atlas montre la persistance d'une suture entre l'intercentre et l'arc neural, et que l'axis est dépourvu de canal transverse et garde des côtes axiales, deux caractères primitifs. La colonne thoracique est non moins généralisée dans son ensemble ; par contre la colonne lombaire est interprétée comme dérivée, en raison de l'allongement progressif du corps vertébral et des apophyses transverses, et de la hauteur des épines neurales dirigées vers l'avant : une telle morphologie ne se retrouve pas chez les didelphides examinés, mais bien chez la forme fouisseuse *Perameles*. Dans ce contexte, le sacrum est considéré comme spécialisé, avec deux vertèbres dont une seulement s'appuie sur l'ilion. La longueur de la queue reste imprécise, mais les vertèbres caudales conservées ne montrent aucune spécialisation préhensile, contrairement à celles d'*Henkelotherium* ou de *Didelphis*.

La ceinture scapulaire est identique à celle des didelphides actuels les plus primitifs ; l'humérus montre une vaste surface d'insertion pour les extenseurs, comme celui des petites formes terrestres ; le cubitus et le radius sont encore très robustes. Les os du carpe et de la main n'ont pas été conservés.

La bassin, bien que massif, présente, comme le sacrum, des spécialisations de type péramélide, avec une grande expansion dorso-ventrale de l'aile antérieure de l'ilion, un grand foramen obturateur, et des os marsupiaux réduits. Au contraire, les os de la cuisse et de la jambe sont plus primitifs que ceux des petits didelphides actuels. L'astragale n'est pas très bien conservé, mais il semble que sa morphologie était plus plésiomorphe que celle de *Didelphis*. Quant au calcanéum, il est dépourvu de facette fibulaire ; il est donc plus évolué que celui définissant le "morphotype métathérien" de SZALAY (1982a, b) et se rapproche du "morphotype didelphide" ; il conserve pourtant un fort processus péronéen, interprété dans ce contexte particulier comme un caractère plésiomorphe. Un point intéressant concerne l'orientation de la facette cuboïdienne, considérée comme annonçant la condition des didelphides actuels. Le pied lui-même paraît avoir été long et relativement rigide.

De l'ensemble de ces caractères, les auteurs déduisent pour *Pucadelphys andinus* un mode de vie terrestre et non arboricole (une adaptation considérée comme primitive pour les Theria Tribosphenida, Krebs, 1991) : l'astragale et le calcanéum en particulier ne montrent pas les caractères reliés à une telle spécialisation ; malheureusement la configuration de la jonction tibia-astragale n'a pu être précisée, nous ignorons donc s'il y avait renversement du pied comme observé par Jenkins & Mc Learn (1984) chez quelques didelphides arboricoles.

Dans le détail, la brièveté des apophyses épineuses des vertèbres cervicales suggère une bonne mobilité du cou. L'étroitesse de l'espace séparant radius et cubitus imposait une rotation limitée de l'avant-bras. Le développement des métapophyses dorsales, la longueur des apophyses épineuses des vertèbres lombaires et la largeur de l'extrémité distale de l'humérus constituent autant de potentialités fouisseuses ; de même, la longueur des épines lombaires et la conformation du sacrum (possible mobilité de la jonction sacro-iliaque, grand angle ilio-sacré, largeur et orientation de la surface iliaque destinée aux abducteurs et extenseurs de la cuisse) devaient favoriser le fouissement, sans qu'une telle spécialisation soit, chez *Pucadelphys*, poussée aussi loin que chez *Perameles*. Par ailleurs les proportions relatives des membres supérieur et inférieur sont compatibles avec une bonne agilité mais ne correspondent pas à celles d'un animal coureur ; enfin cette espèce semble avoir été capable de sauter, mais sans être réellement spécialisée dans cette direction.

En ce qui concerne le mode de vie, cette forme devait être nocturne comme la plupart des petits didelphides, dormant le jour dans un nid-terrier et cherchant sa nourriture durant la nuit. La connaissance des mœurs des petits didelphides actuels (qui sont habituellement solitaires) conduit à penser que ces quatre squelettes associés deux à deux représentent ceux de couples formés durant la période de reproduction ; les terriers étaient creusés dans la berge d'une rivière, dont la crue subite a rempli ces nids de sédiments ayant favorisé la conservation en position naturelle. Cette conclusion est corroborée par l'abondance des fossiles trouvés dans le gisement (comportant en particulier des squelettes presque complets de grenouilles).

Peu de caractères du squelette permettent de préciser la position phylogénique de *Pucadelphys andinus*, si ce n'est la configuration du tarse. Celle-ci, jointe aux conclusions concernant le crâne et la denture, font considérer *Pucadelphys* comme le taxon le plus plésiomorphe à l'intérieur des Didelphidae.

INTRODUCTION

Postcranial bones of mammals are very important in phylogenetic studies; yet these elements are extremely rare in rocks of Cretaceous and Paleocene age, a time when the basic branches of this class became established. Associated skeletons which provide functional and phylogenetic information are even rarer, and those with associated dentitions and skulls are almost non-existent. Because of a dearth of such specimens, little is known of the early postcranial evolution of Tribosphenida (metatherians, eutherians and related forms with tribosphenic dentitions; *sensu* McKenna, 1975). In fact, the postcranial character states in the direct ancestor(s) of metatherians and eutherians are currently inferred from the study of all too few isolated Cretaceous and Paleocene elements, of Eocene to Pleistocene fossils, and of living taxa.

There are, to date, only two non-tribosphenid therians (both eupantotheres) for which associated postcranial material is known. One is *Henkelotherium guimarotae* from the Late Jurassic of Portugal, described by Krebs (1987; 1991), and the other is *Vincelestes neuquenianus* from the Early Cretaceous of Argentina, which is not yet described (see Bonaparte & Rougier, 1987 ; Rougier *et al.*, 1992 ; Wibble & Hopson, 1993).

Eutherians are the best known of Late Cretaceous tribosphenids, and partial skeletons of *Asioryctes*, *Zalambdalestes* and *Barunlestes* have been described from the ? Late Santonian and/or Campanian of Asia (Kielan-Jaworowska, 1977, 1978).

In contrast, postcranial remains of metatherians from the Late Cretaceous and Paleocene are presently known only from isolated calcanea and astragali (Szalay, 1982a and b; 1984); associated skeletons have not been reported. The earliest nearly complete skeleton of a metatherian

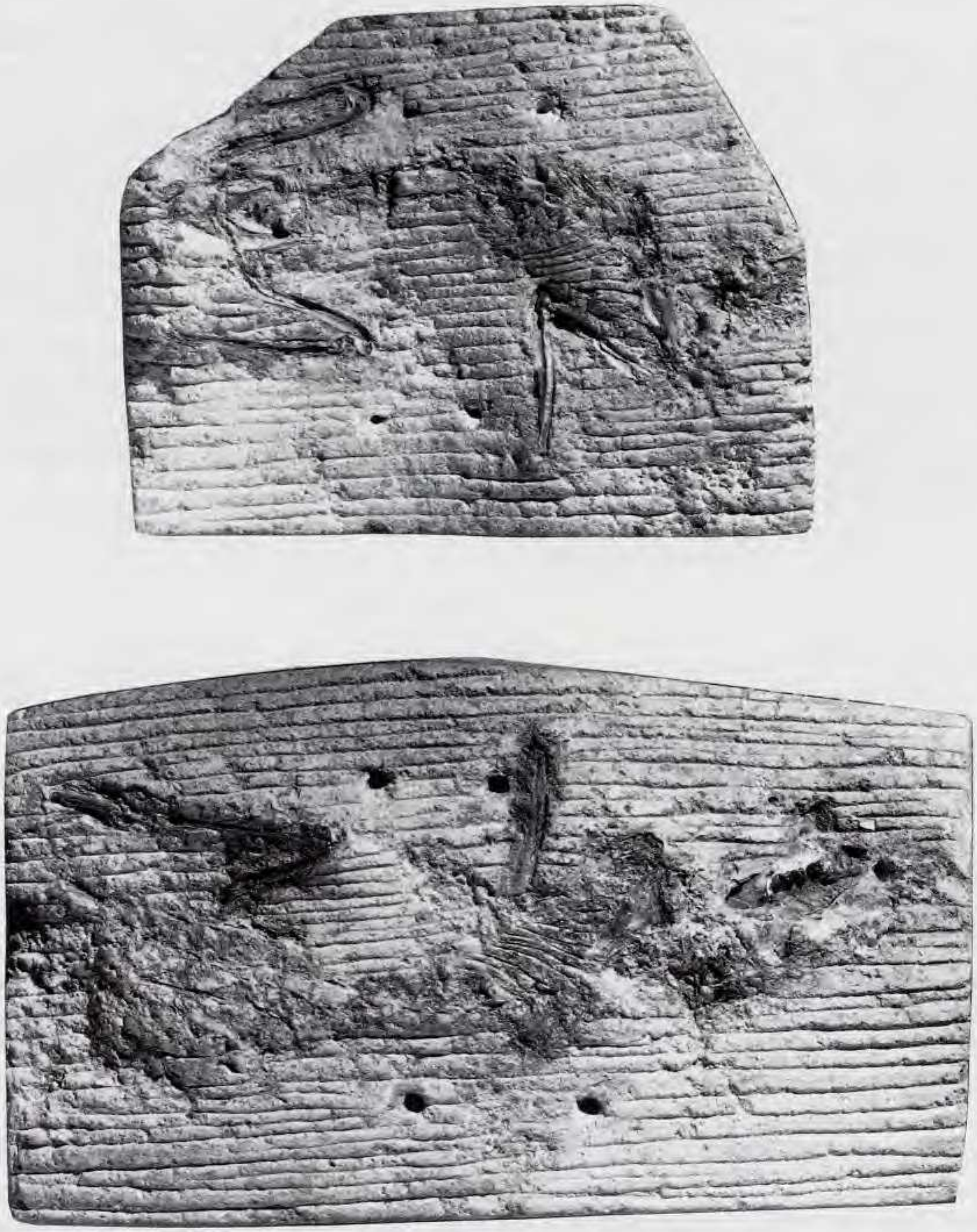


FIG. 22. — The "sarigue fossile" from Montmartre, CUVIER collection MNHN 7905 (top) and 7904 (bottom): opposite halves of same specimen, type of *Peratherium cuvieri* Fischer, 1829. X 1.

FIG. 22. — La sarigue fossile de Montmartre, collection CUVIER *MNHN 7905 (haut) et 7904 (bas): moitiés opposées du même spécimen, type de* Peratherium cuvieri *Fischer, 1829. X 1.*

FIG. 23. — The "sarigue fossile" from Montmartre (after CUVIER 1804, Pl. 19), type of *Peratherium cuvieri (*Fischer, 1829).

FIG. 23. — La sarigue fossile de Montmartre (d'après CUVIER 1804, Pl. 19), type de Peratherium cuvieri *(Fischer, 1829).*

Source : MNHN, Paris

was long represented by the classic "sarigue fossile" collected from the Butte Montmartre in northcentral Paris (Figs 22, 23). The fossil is from the "Gypse de Montmartre", assigned to the Late Eocene (*i.e.* Headonian Land Mammal Age, Savage *et al.*, 1994). It was first described by Cuvier (1804), named *Didelphis cuvieri* by Fischer (1829), and is now classified as *Peratherium cuvieri* (Crochet, 1980).

Hence the major interest of the four nearly complete skeletons, two of which have articulated skulls, of the metatherian *Pucadelphys andinus*, from the Early Paleocene Santa Lucía Formation at Tiupampa in southcentral Bolivia. These are currently the earliest and most complete articulated skeletons of metatherians yet known, and they provide the first opportunity to securely assess aspects of the postcranial structure of a member of this group at the "Beginning of the Age of Mammals".

Unless otherwise specified, all numbers cited below, in the figure captions and in the Appendix (i.e. 6105, 6106, 6110, 6111) pertain to YPFB.

SYSTEMATIC PALEONTOLOGY

The skeleton-pairs described in this study were collected with articulated skulls, one of which (6105) was designated the type of *Pucadelphys andinus* Marshall & Muizon, 1988. A detailed study of the dentitions and skulls of 6105 and 6110 (as well as numerous other specimens), shows that both skeleton-pairs are referable to this species (Marshall & Muizon, 1995). The systematic position of the skeletons is thus as follows:

Legion TRIBOSPHENIDA McKenna, 1975
Infraclass METATHERIA Huxley, 1880
Order DIDELPHIMORPHIA (Gill, 1872) Marshall *et al.*, 1989
Family DIDELPHIDAE Gray, 1821
Genus *PUCADELPHYS* Marshall & Muizon, 1988

Pucadelphys andinus Marshall & Muizon, 1988

Diagnosis (postcranial skeleton morphology only). — Atlas not perforated by transverse canal, and with a persisting suture between ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; lumbar series specialized compared to that of other didelphids (gradual lengthening of vertebral body and transverse processes, long anteriorly directed neural spines); single fulcral vertebra (Sl); specialized pelvis (ilium dorsoventrally expanded anteriorly, large obturator foramen, small ossified os marsupium); possible movable sacro-iliac joint; long (±30 caudals) non-prehensile tail; digging specializations of the humerus (no third distal articular surface, large areas for extensors of forearm and carpus); robust fibula; calcaneum with bicontact upper ankle joint (UAJ) (Szalay, 1982a, b), large peroneal process and remarkably broad transverse dimensions from peroneal process to medial margin of sustentaculum.

DESCRIPTION

Measurements (in mm) of the individual bones of the specimens of *Pucadelphys* described below are given in Tables 1 to 20 in the Appendix.

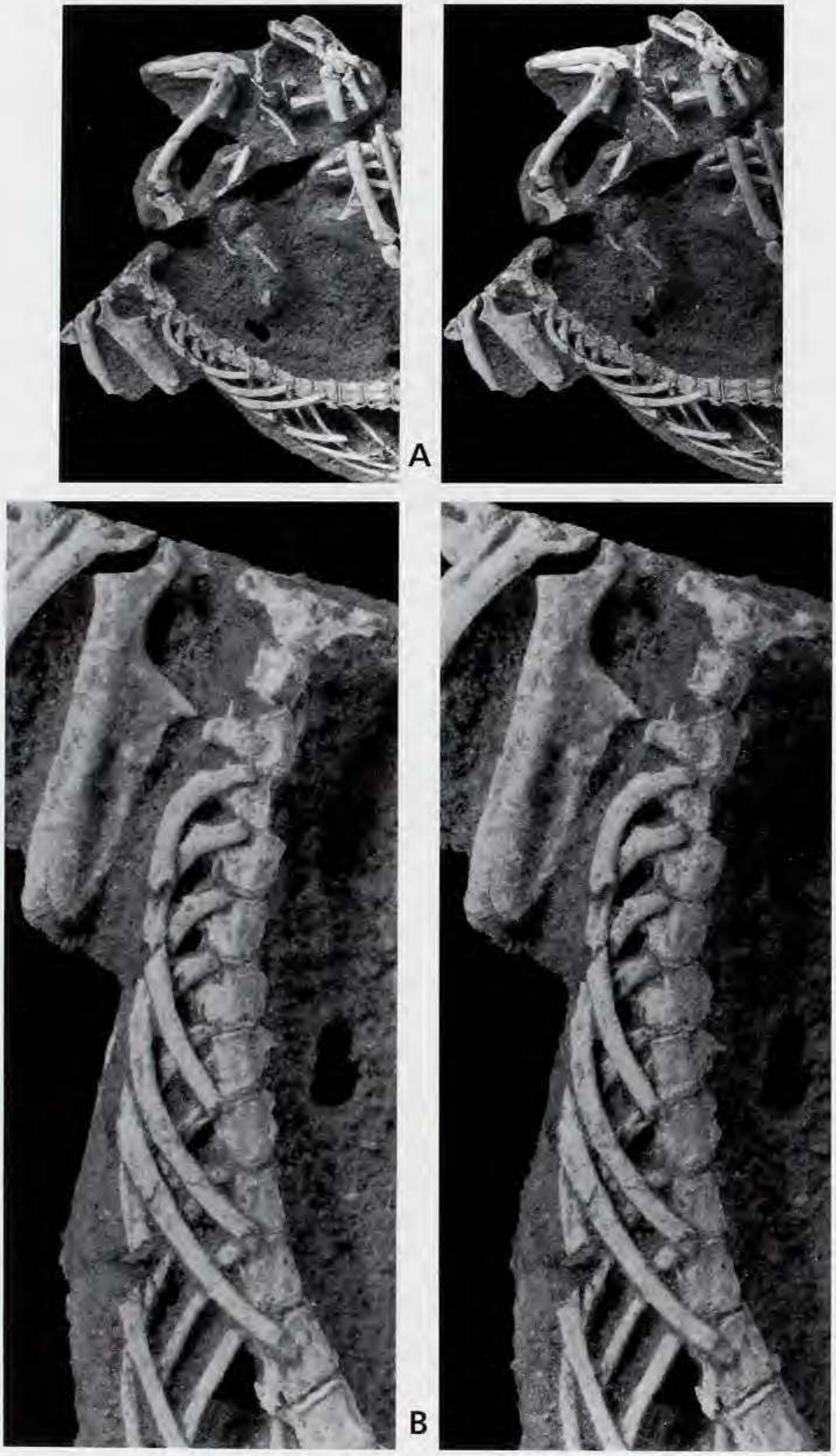
General Features. — Skeleton-pairs YPFB Pal 6105 and 6106 (Figs 2, 24A and 25A). The animals are in a snout-rump position; 6105 faces to the right and 6106 to the left (referring to the positions as in the photos). Part of the dorsal surface and the entire ventral surface of both individuals are presently visible, and the latter was presumably on the floor of the burrow when the animals died and were fossilized. Both individuals are adults as evidenced by the facts that the skull of 6105 has a slightly worn adult dentition and the epiphyses, although still distinct, are all firmly attached to the diaphyses. 6106 is slightly larger than 6105 (see Appendix).

On 6105, the seven cervical and eleven thoracic vertebrae are in a nearly straight line. The left forelimb is extended posteriorly and parallel along the body. The left hindlimb (as seen on the opposite surface of the block) has the femur on top of the thoracic region of 6106, the tibia and fibula extend posteriorly over the thoracic vertebrae to T11, and the pes is on the right side of that specimen. These features indicate that the pelvic region of 6105 was lying upon the upper thoracic, neck and possibly head region of 6106.

On 6106, the body is in an arched position as shown by the arrangement of the articulated Tl to C9 vertebrae. The right forelimb lies along side and nearly parallel to the body and, as shown by the humerus, was extended posterolaterally. The proximal part of the left forelimb is extended anterolaterally under the posterior lumbar-pelvic region of 6105, with the ulna and radius flexed sharply anteriorly along the posterolateral side of 6105. The right hindlimb is flexed anteriorly under the abdominal area. The left hindlimb is extended laterally, with the tibia and fibula under the thoracic region of 6105.

Skeleton-pairs YPFB Pal 6110 and 6111 (Figs 3, 4 and 26). The animals are also in a snout-rump position; 6110 faces to the right and 6111 to the left (referring to the positions as in the photos). The dorsal surfaces of both individuals are visible. Both individuals are subadults as demonstrated by the facts that the skull of 6110 has an unworn adult dentition and the epiphyses are unfused and often separated from the diaphyses in both individuals. 6110 is slightly larger than 6111 (see Appendix) and both individuals are notably smaller (average about 20%) than 6105 and 6106.

On 6110, the pelvic area is nearly horizontal. The tail bends sharply dorsolaterally to the left and the end of the tail lies upon, and parallels, the thoracic vertebrae of 6111. In the posterior thoracic region the body begins to twist to the left, with the cervicals and head completely on their left side. The proximal end of the right forelimb is extended posterolaterally and the ulna is flexed sharply anteriorly. The left forelimb extends parallel along the posterior side of the proximal part of the right forelimb. The relationship of the forelimbs and cervical vertebrae clearly shows that the animal was lying on its left shoulder. The right hindlimb was extended nearly perpendicular to the body, while the left hindlimb was in a tightly anteriorly flexed position directly under the body.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B

6111 was lying on its right shoulder with the right forelimb extending nearly perpendicular on the left side of the body (as seen by the position of the distal end of the humerus and proximal ends of the ulna and radius). The left forelimb was flexed tightly against the thoracic region of the right side of the body and the "elbow" abuts vertebrae T8 and T9. The proximal end of the right hindlimb extends anteriorly under the body such that the femur parallels the lumbar vertebrae and the distal end (tibia and fibula) extends nearly perpendicular on the left side of the body. The left hindlimb is extended anterolaterally on the left side of the body, and the distal parts of the tibia and fibula (and pes) lie upon the lumbar region of 6110.

Collectively, the four specimens include about 95% of the complete skeleton. The only missing elements are the manus (see p.127), the first metatarsal, some tarsals and phalanges of the pes, and an estimated 17 posterior caudal vertebrae.

AXIAL SKELETON.

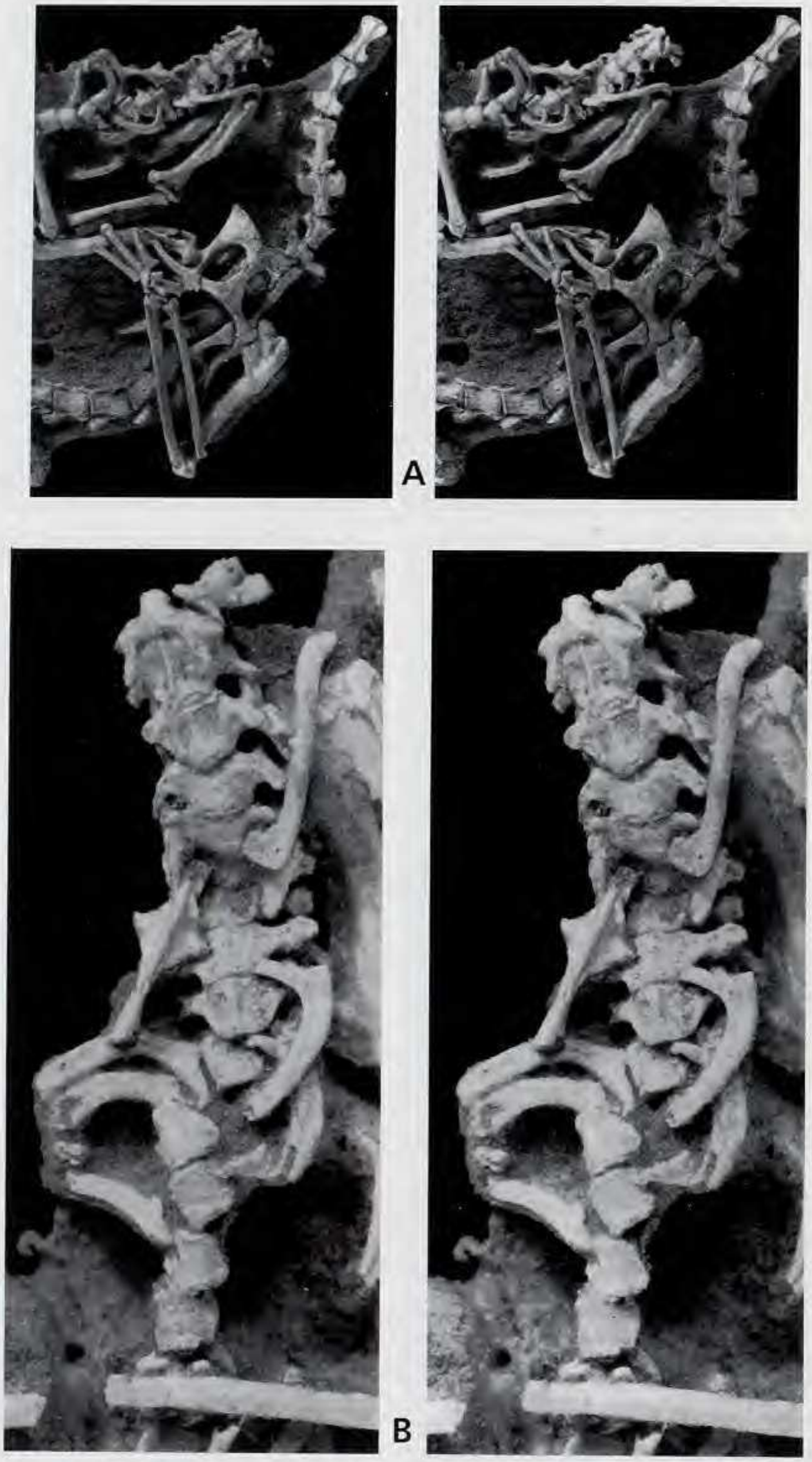
6105	7 cervicals (left half of atlas, axis, CV3-CV7) 9 thoracics (T1-T9, fragments of T10-T11)
6106	13 thoracics (T1-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C9)
6110	7 cervicals (atlas, axis, CV3-CV7) 8 thoracics (T6-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C5, C16?-C17?, C20?-C21?)
6111	7 thoracics (T7-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C9)

CERVICAL VERTEBRAE

Atlas (Figs 25B, 27 and 28A, B; Table 1).— Two elements: 6105, left half (attached to axis), ventral and lateral views; 6110, isolated left and right halves, nearly complete.

FIG. 24. — *Pucadelphys andinus.* Stereophotos. A, specimen-pair 6105-6106, partial view. X 1; B, 6106, right scapula, anterior view; thoracic vertebrae and ribs, ventral view. X 3.

FIG. 24. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6105-6106, vue partielle. X 1; B, 6106, omoplate droite, vue antérieure; vertèbres thoraciques et côtes, vue ventrale. X 3.*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The dorsal arch (da) is narrow ventrally and considerably broader dorsomedially. Laterally, the dorsal arch joins the base of the ventral arch and projects as a flat, horizontal, ovoid transverse process (6105), constricted at the base. In 6110, only the root of the transverse process is preserved on both halves (b tp); but the lateral-most surface does not appear to be broken, suggesting that the transverse process had a different center of ossification and fused with the root only in adults. Anterior to the transverse process, the articular facet for the occipital condyle (lf of) is wide and distinctly concave; posterior to it, the articular facet for the atlas body (i.e. anterior part of the axis *sensu lato*) is smaller and only slightly concave (ax f). The two articular facets (for occipital and atlas body) are not situated directly opposite each other anteroposteriorly: the occipital facet slopes posteromedially at an angle of about 40°, while the atlas body facet is more transverse and faces mostly posterolaterally at an angle of about 33°. As for the ventral component of the atlas (intercentrum), what must be its lateral part appears to be suturally joined to the left atlas of 6105 and directed towards the ventral surface of the dens. Supporting this interpretation is the presence of a facet on the posteroventromedial edge of the atlas arch of 6110, immediately adjacent to the articular facet for the atlas body of the axis (Fig. 27C, si); we thus assume that the intercentrum was ossified in the adult. The groove for the vertebral artery at the anterior base of the dorsal arch is deep in the adult 6105 and shallower in the subadult 6110 (t s). Behind the transverse process, a deeper sulcus (for "neuro-vascular structures" according to Jenkins & Parrington, 1976) separates the latter from the axial facet. A very small canal is clearly visible on the right side of 6110 (t c?), the posterior opening of which, just behind the root of the transverse process, being larger than the anterior one which is in front of the same process; whether this is homologous to a transverse canal remains uncertain (see discussion p. 111). The atlantal canal for cranial nerve I, situated on the medial side of the occipital facet, is not closed.

Axis (Figs 25, 28C-E, 29A and 38A; Table 1). — Two elements: 6105, ventral, medial and left lateral views; 6110, all surfaces visible.

The suture between the atlantal and axial component is distinct in 6110 on the dorsal and ventral surface of the body, while in 6105 it only appears as an elevated transverse ridge on the ventral surface, but is still distinct on the dorsal surface. The atlas component of the axis body is wider than the axial part. Both components have two (paired) distinct nutrient foramina on the dorsal face of the body. The dens is oriented anterodorsally, is slightly flattened dorsoventrally, and transversely convex both dorsally and ventrally. A distinct medial keel extends longitudinally along the ventral surface of the body and posteriorly forms a broad lip. Lateral to the medial keel are two broad depressions which are bordered by the ventral root of the transverse processes (Fig. 28, tp v). The neural arch (6105) is very long dorsally relative to its ventral base; hence the anterior

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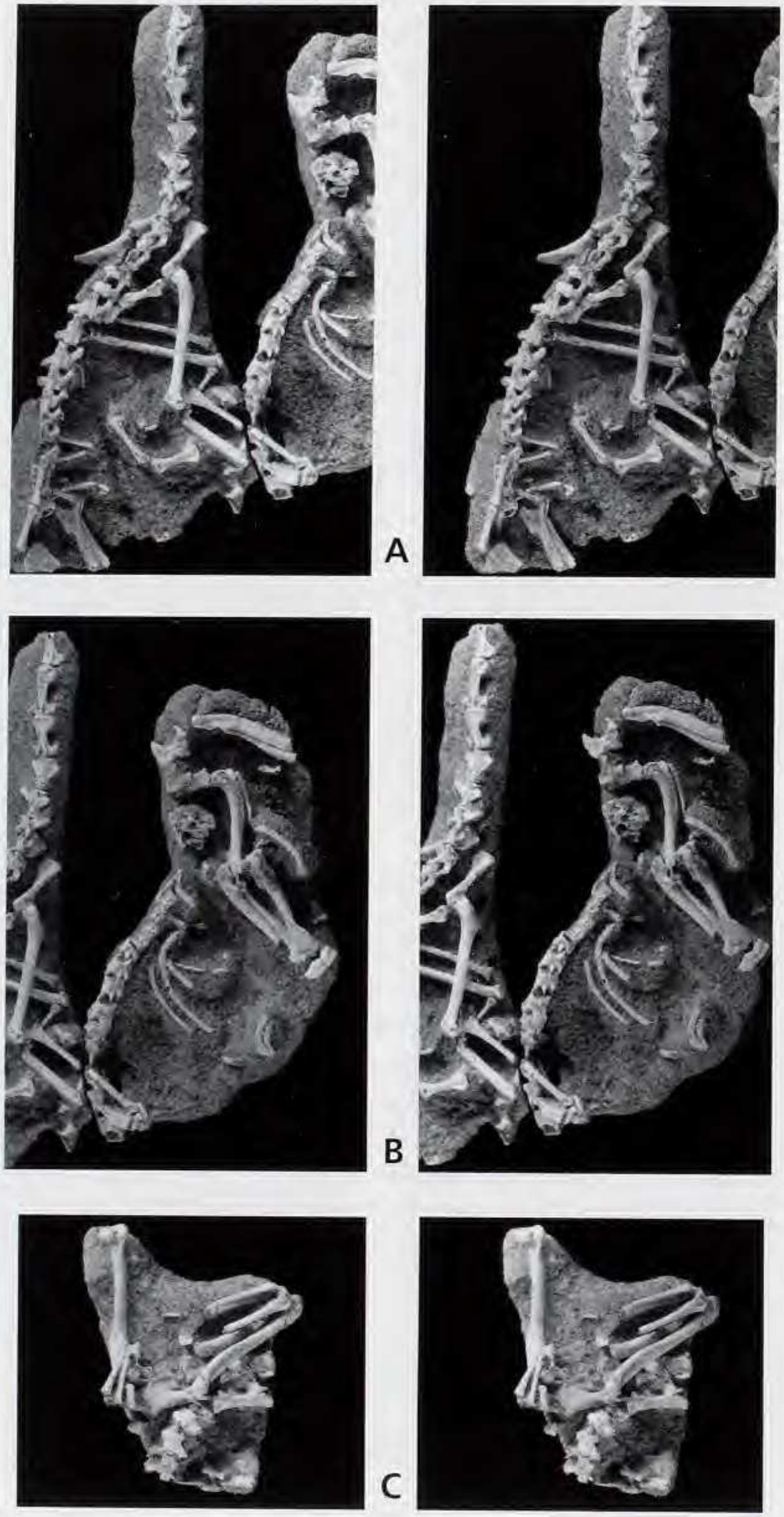
Fig. 25. — *Pucadelphys andinus*. Stereophotos. A, specimen-pair 6105-6106, partial view. X 1; B, 6105, cervical vertebrae, interclavicle and left clavicle, ventral view. X 3.

Fig. 25. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6105-6106, vue partielle. X 1; B, 6105, vertèbres cervicales, interclavicule et clavicule gauche, vue ventrale. X 3.*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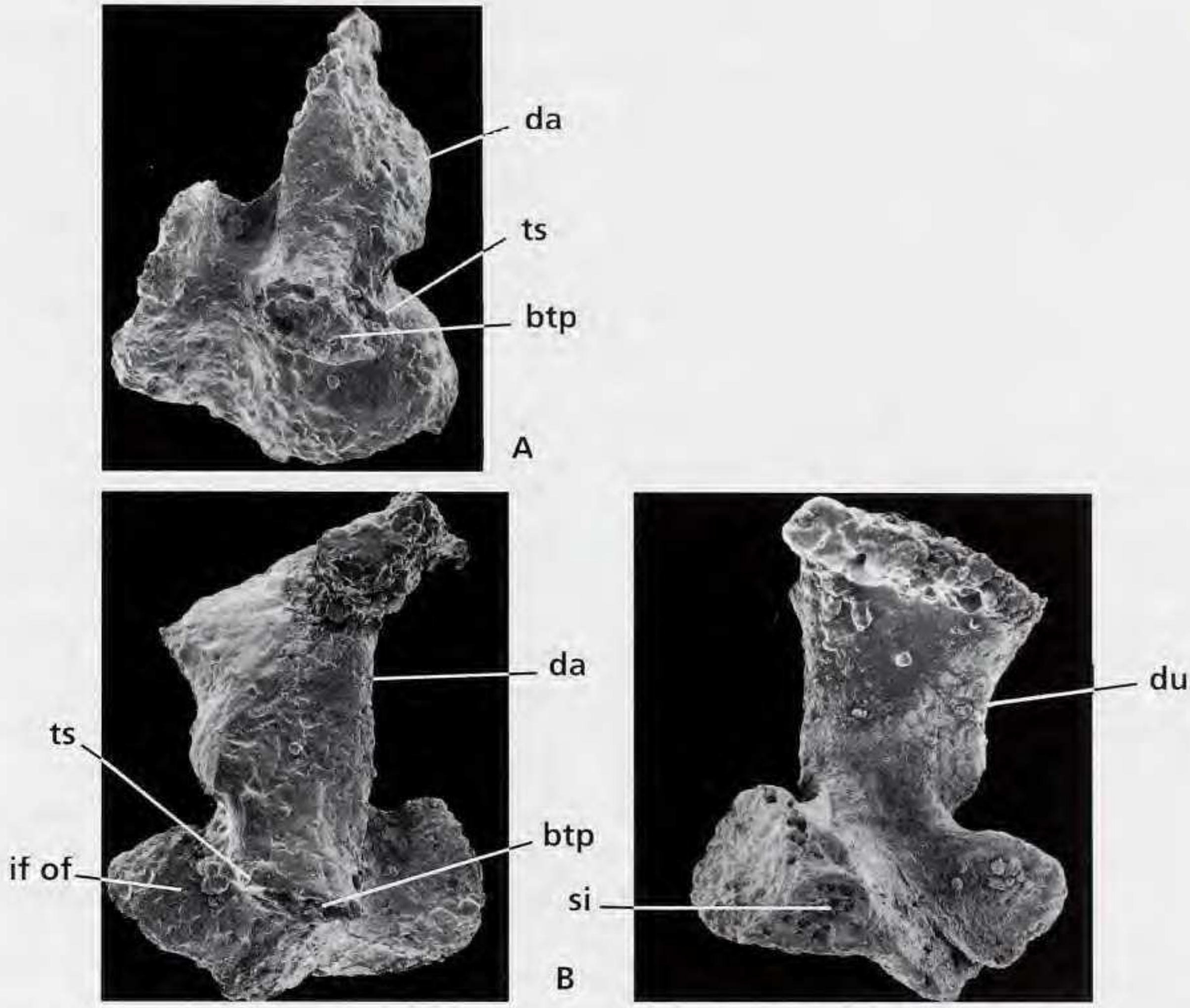


FIG. 27. — *Pucadelphys andinus*. 6110, atlas: A, right half, lateral view; B, left half, dorsolateral view; C, left half, mesial view. X 13,5. Abbreviations: **b tp**, base of transverse process; **d a**, dorsal arch; **lf of**, lateral face of occipital facet; **si**, surface for intercentrum; **t s**, transverse sulcus.

FIG. 27. — Pucadelphys andinus. *6110, atlas: A, moitié droite, vue latérale; B, moitié gauche, vue dorso-latérale; C, moitié gauche, vue mésiale. X 13,5. Abréviations:* ***b tp****, base du processus transverse;* ***d a****, arc dorsal;* ***lf of****, face latérale de la facette occipitale;* ***si****, surface pour l'intercentre;* ***t s****, sillon transverse.*

FIG. 26. — *Pucadelphys andinus*. Stereophotos. A, specimen-pair 6110-6111, partial view. X 1; B, the same, partial view. X 1; C, 6110, posterior vertebrae and hindlimb: this block appeared to represent the posterior part of 6110 only after preparation; but the ventral surface of this block had been prepared, while on the main block the preparation was of the opposite surface; in order to link the two blocks, it is necessary to reverse C and also turn it 90° (see Figs 3 and 4). X 1.

FIG. 26. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6110-6111, vue partielle. X 1; B, le même, vue partielle. X 1; C, 6110, vertèbres postérieures et membre postérieur: ce bloc ne s'est révélé représenter la partie postérieure de 6110 qu'après préparation; mais c'est la surface ventrale de ce bloc qui avait été préparée, alors que sur le bloc principal la préparation portait sur la face opposée; afin de relier les deux blocs, il a donc été nécessaire de renverser C et de le tourner de 90° (voir figs 3 et 4). X 1.*

border is deeply concave and the atlanto-axial intervertebral space is large. The posterior border of the neural arch is straight. The spine itself is not intact but was low, long and thin; anteriorly it overhangs the vertebral body (dens not included); posteriorly it only slightly overhangs CV3. The anteriorly facing atlantal facets (at f) are oval, short and directed almost vertically. The postzygapophysial facets face lateroventrally. The transverse process had two roots which, as seen on 6105, did not unite laterally; as a result the transverse "canal" between the two roots remains a wide sulcus (t s). The lateral extremity of the dorsal root on both sides of 6105 is uniformly concave and does not appear to have been broken; this may have been the attachment surface for a small cervical rib, a remnant of which may be represented by the bone fragment located along the anterior surface of the dorsal root of CV3 of 6105.

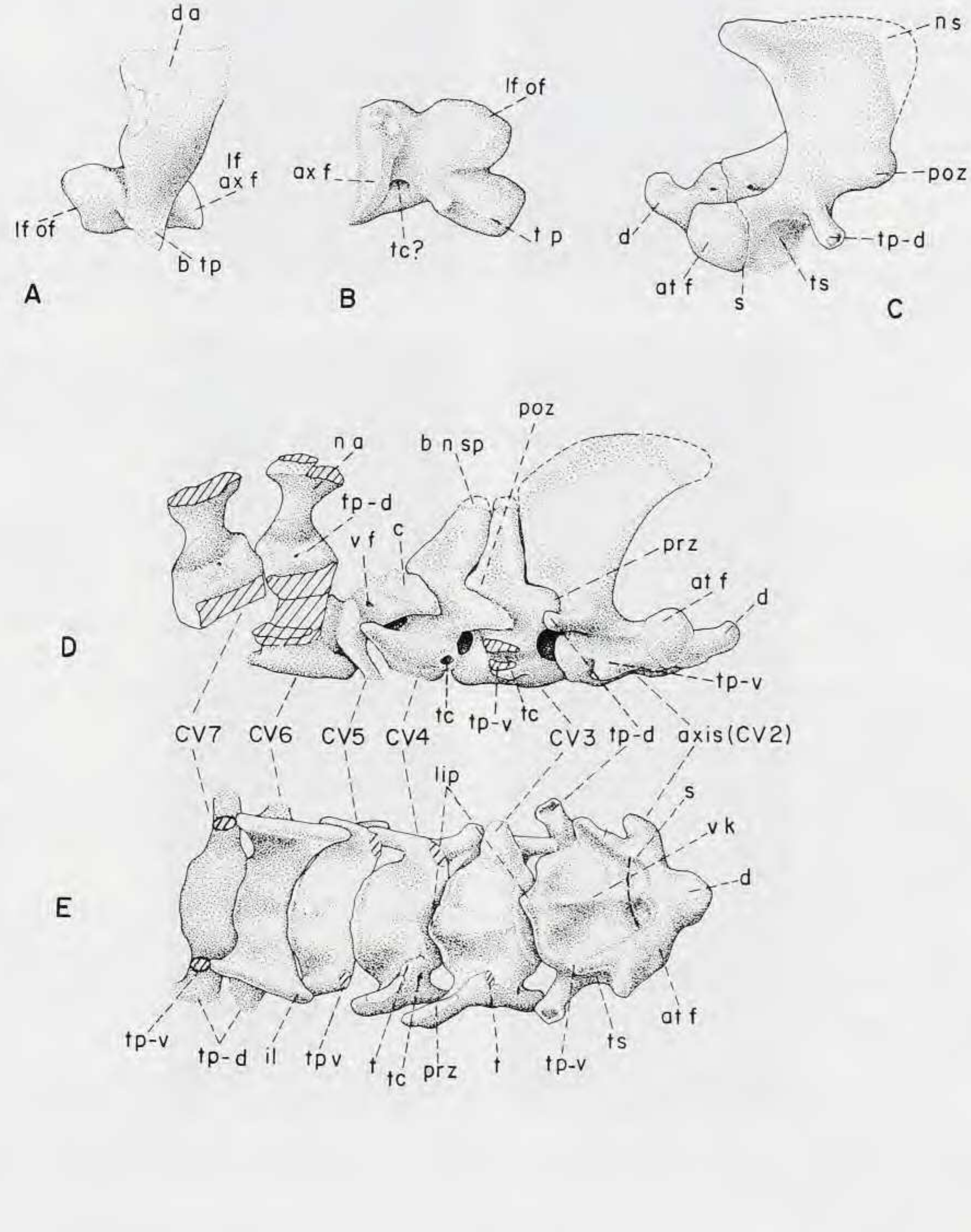
Cervicals 3 to 7 (Figs 25, 28D-E and 29A; Table 2). — Two series: 6105, CV3-7; 6110, CV3-7 (fragmentary).

The epiphyses on all elements remain distinct. CV3 is notably longer than CV4 and both are slightly larger than CV5-CV7, which are also subequal in length. The intervertebral spaces narrow from CV3 to CV7. The zygapophysial facets are only slightly inclined lateroventrally on CV3, and become nearly horizontal on CV4 (not preserved on CV5 to CV7). The vertebral bodies are low and wide, and the spine was apparently short (only the base is preserved on CV3-CV5). The two roots of the transverse process of CV3 to CV6 unite laterally, enclosing the transverse canal (t c); together they produce a thick posterior process, while the ventral root has also an anteroventral projection or tubercle (t). There are no free cervical ribs.

CV3 has a distinct median ventral keel which broadens posteriorly and ends in a wide lip; a nutrient foramen pierces the base of the keel. The lateral depressions are well developed, but shallower than those on the axis. The anterior projection of the ventral root of the transverse process is reduced to a tubercle (Fig. 28E, t). The spinous process is nearly vertical, very short, and the anterior border of the arch is closely appressed to the posterior border of the axial arch, suggesting that there may have been some contact between the two arches.

FIG. 28. — *Pucadelphys andinus*. A-B, atlas: A, 6110, left half, dorsolateral face; B, 6105, left half, ventral face; C, 6110, axis, left lateral face; D-E, 6105, cervical vertebrae CV2-CV7; D, right lateral face; E, ventral face. All drawn as preserved. X 8. Abbreviations: **at f**, atlantal facet; **ax f**, axial facet; **b n sp**, base of neural spine; **b tp**, base of transverse process; **d**, dens; **d a**, dorsal arch; **il**, inferior lamella of CV6; **lf ax f**, lateral face of axial facet; **lf of**, lateral face of occipital facet; **n a**, neural arch; **n s**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis, **s**, suture between atlantal and axial component; **t**, tubercle, see text; **tc**, transverse canal; **t p**, transverse process, **tp-d**, dorsal root of transverse process; **tp-v**, ventral root of transverse process; **ts**, transverse sulcus; **v f**, vascular foramen; **v k**, ventral keel.

FIG. 28. — Pucadelphys andinus. *A-B, atlas: A, 6110, moitié gauche, face dorso-latérale; B, 6105, moitié gauche, face ventrale; C, 6110, axis, face latérale gauche; D-E, 6105, vertèbres cervicales CV2-CV7: D, face latérale droite; E, face ventrale. Dessin en l'état de conservation. X 8. Abréviations:* ***at f***, *facette atlantale;* ***ax f***, *facette axiale;* ***b n sp***, *base de l'épine neurale;* ***b tp***, *base du processus transverse;* ***d***, *dens;* ***d a***, *arc dorsal;* ***il***, *lamelle inférieure de CV6;* ***lf ax f***, *face latérale de la facette axiale;* ***lf of***, *face latérale de la facette occipitale;* ***n a***, *arc neural;* ***n s***, *épine neurale;* ***poz***, *postzygapophyse;* ***prz***, *prézygapophyse;* ***s***, *suture entre les composants atlantal et axial;* ***t***, *tubercule, voir texte;* ***tc***, *canal transverse;* ***t p***, *processus transverse;* ***tp-d***, *racine dorsale du processus transverse;* ***tp-v***, *racine ventrale du processus transverse;* ***ts***, *sillon transverse;* ***v f***, *foramen vasculaire;* ***v k***, *carène ventrale.*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CV4 has a broad, low, median ventral thickening that widens considerably posteriorly (it is nearly as wide as the posterior epiphysis); the lateral depressions are thus reduced and very shallow. The anterior tubercle of the ventral root of the transverse process is quite prominent. The neural arch is similar to that of CV3 and had probably some contact with that of CV2. The spine itself was very short.

CV5 is flat ventrally. The anterior tubercle of the ventral root of the transverse process is broken, but it was clearly longer than that of CV4; the dorsal root is covered by the inferior lamella (lamina ventralis) of CV6 (Fig. 28 D-E, i l). The left part of the dorsal arch is preserved (6105); its anterior and posterior borders are straight.

Between the two inferior lamellae of CV6 (the anterior part of which corresponds to the elongation of the above mentioned tubercle and the posterior part to the ventral component of the posterior process), the vertebral body is slightly concave; the expansion of the dorsal root of the transverse process is here separated from its ventral counterpart and is oriented more laterally than posteriorly.

On CV7, the ventral surface of the centrum has a low longitudinal median ridge and very shallow lateral depressions. The dorsal root of the transverse process is now completely laterally oriented, the ventral root is reduced to a small spine, and the two roots are not fused (i.e. the "transverse canal" is open laterally).

Thoracic vertebrae (Figs 24B, 29B, 30, 32A and 47A, B; Table 3). — Present in all four specimens: 6105, Tl to T9, ventral view (although T5 to T9 are represented only by ventral part of centra); 6106, T1 to T13, ventral and both lateral views; 6110, dorsal views of ventral half of T6 to T9, dorsal and both lateral views of T10 to T13; 6111, T12 and T13, dorsal and partial lateral views.

The presence of a small transverse process on the 14th dorsal (*i.e.* L1) demonstrates that there are 13 thoracic vertebrae.

As seen best in 6106, the vertebral body increases slightly in length from T1 to T13. T1 to T4 have a longitudinal median keel which is broad and low on Tl, higher and narrower on T2 to T4. The vertebral body is ventrally angular on T3 to T5, convex on T6 and T7, flat on T8 and T9, and with a longitudinal median trough bordered by low broad lateral ridges on T10 to T13 (a feature progressively developed from T10 to T13).

The neural spine is broken on all exposed vertebrae, except T1, T11 and T12 of 6106, and T9 and T10 of 6111 where it is low, narrow (it thickens at the top) and inclined slightly posterodorsally; it arose on the posterior half of the arch and was transversely thin at the root. The articular surfaces of the dorsal zygapophyses become more vertical posteriorly and are widely separated.

On T1 and T2, the transverse processes which bear the parapophyses for the ribs are ventrally situated opposite the anterior end of the body; they are flat and project quite far laterally, flaring slightly after a constriction at the root. Beginning on T3 they arise more medially on the body, and are also more dorsally situated due to the ventral angulation of the body; they become shorter from T5 to T7, and on T8 (and those more posteriorly), they merely constitute a less and less prominent facet on the lateral side of the body, to become undistinguishable on T11-T12.

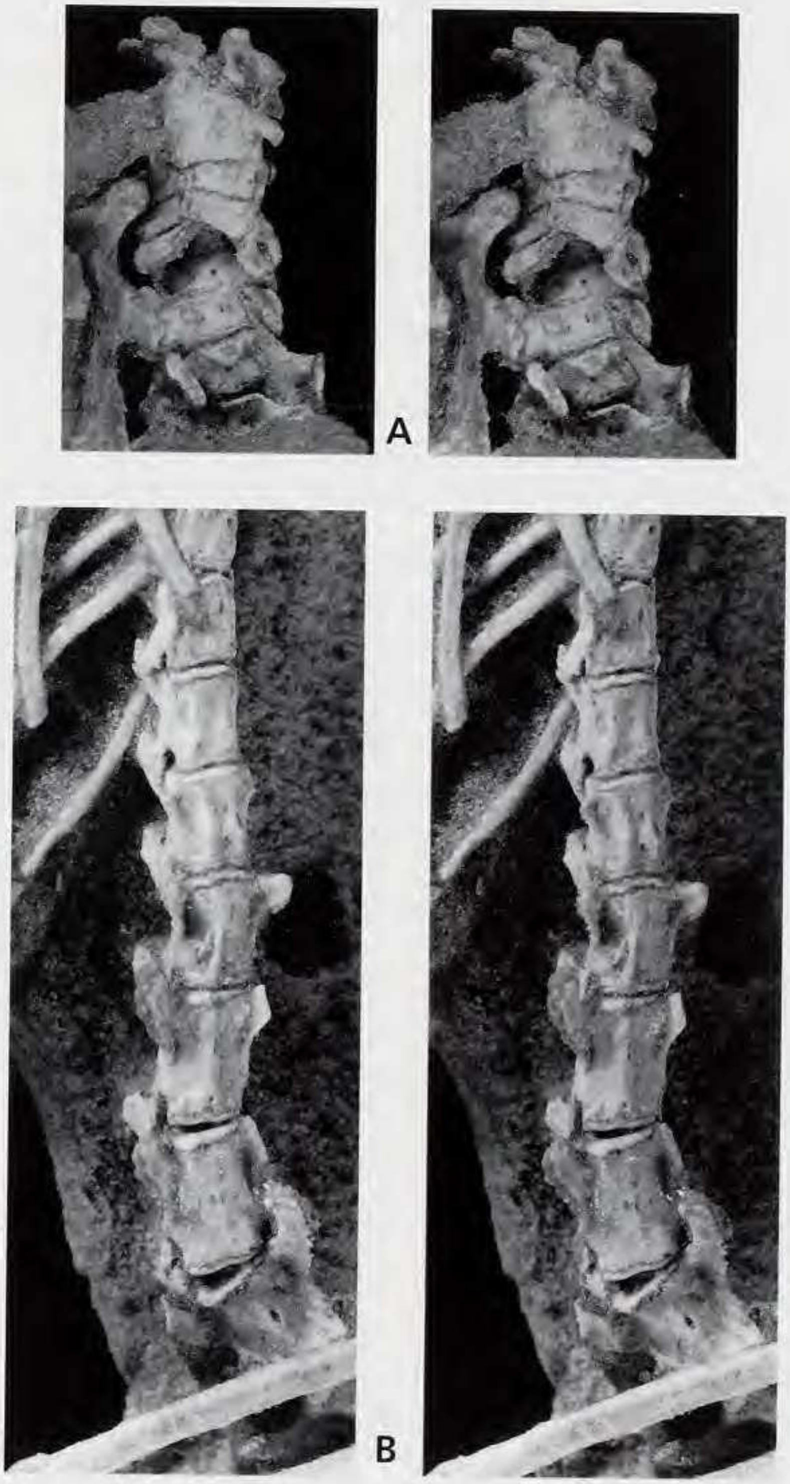


FIG. 29. — *Pucadelphys andinus*. Stereophotos. A, 6105, cervical vertebrae, dorsal view. X 3; B, 6106, vertebrae T10-L4, ventral view. X 3.

FIG. 29. — Pucadelphys andinus. *Stéréophotos. A, 6105, vertèbres cervicales, vue dorsale. X 3; B, 6106, vertèbres T10-L4, vue ventrale. X 3.*

T8 is a transitional vertebra with the appearance of the first anapophysis (ap) and the first metapophysis (mp). These apophyses become progressively longer from T9 to T13; they interlock and produce a secondary articulation at least from T10 to T13. The costal facets are not clearly discernible on the vertebral bodies.

Ribs (Fig. 24). — There are 13 pairs of ribs. The first nine pairs have tuberculae and capitulae, while the last four pairs lack tuberculae. The distal ends of all ribs are broken, so it is not possible to determine their exact length. The parts that are preserved consistently show a lack of curvature along the ventral half, indicating the presence of a relatively deep chest cavity. They are narrow, proximally compressed anteroposteriorly, with a faint longitudinal sulcus.

Lumbar vertebrae (Figs 29B, 30, 31, 32 and 41; Table 4). — Complete series (L1 to L6) in three specimens: 6106, ventral, lateral and partial dorsal views; 6110, dorsal, ventral and lateral views (L2 and L3 are damaged); 6111, dorsal, lateral and partial ventral views.

The vertebral body of the lumbars (especially of LI) is very much like that of the last thoracics, only deeper; its length increases from L1 to L4. There are usually two nutrient foramina (Fig. 32B, n f) on the ventral body surface of all lumbars, but they are more irregularly situated than those on the thoracics. The ventral surface of L1 has a shallow median longitudinal depression bordered by low broad lateral ridges, almost identical to the condition of T13; on L2 the two ridges are closer and on L3 they meet in a median longitudinal crest; L4 to L6 are gently convex transversely. The anterior and posterior rims curve slightly ventrally, producing an incipient "saddle-shape", and the body is completely platycoelous, at least posteriorly.

The neural spine, as seen on 6106, is very narrow anteroposteriorly (Fig. 31); it is dorsally directed on L1 and L2, and sharply inclined anteriorly on L3 to L6; it increases markedly in height from L1 to L4 (L4 to L6 are subequal). Due to bifurcation of the posterior base of the neural spine, the latter is more anteriorly situated on L4 to L6 and a basal sulcus develops along its posterior border.

The zygapophyses are more robust and clearly more inclined than on the thoracics, with articular facets almost vertical. The meta- and anapophyses are longer than on the thoracics, as are the "trous de conjugaison". These metapophyses are tightly interlocked with the zygapophyses (Fig. 30C).

The narrow and thin transverse processes (tv p) increase sharply in size from L1 (where they are only incipiently developed) to L6; they are inserted anteriorly on the body, all anteriorly directed, and project more and more ventrally from L2 to L6 where they make a sharp angle with the body.

Sacral vertebrae (Figs 31, 32 and 41; Table 5). — Three specimens: 6106, complete in ventral view (though slightly masked by underlying bones) and partly visible in dorsal view; 6110, ventral view of Sl and part of S2; 6111, dorsal view, but dorsal wall of vertebral body is broken on posterior half of Sl and all of S2 (thus is visible the dorsal half of the ventral vertebral body).

The sacrum consists of two vertebrae which together form a short and wide triangle ("apex" points posteriorly), but only S1 contacts the ilium (fulcral vertebra). The vertebral body

Source : MNHN, Paris

of S2 is longer than that of S1, as well as that of C1. The dorsal intervertebral foramen, elongate between L6 and S1, is very small between S1 and S2, and S2 and C1. The suture between S1 and S2 is distinct, and so is the ossification fissure between body and epiphyses.

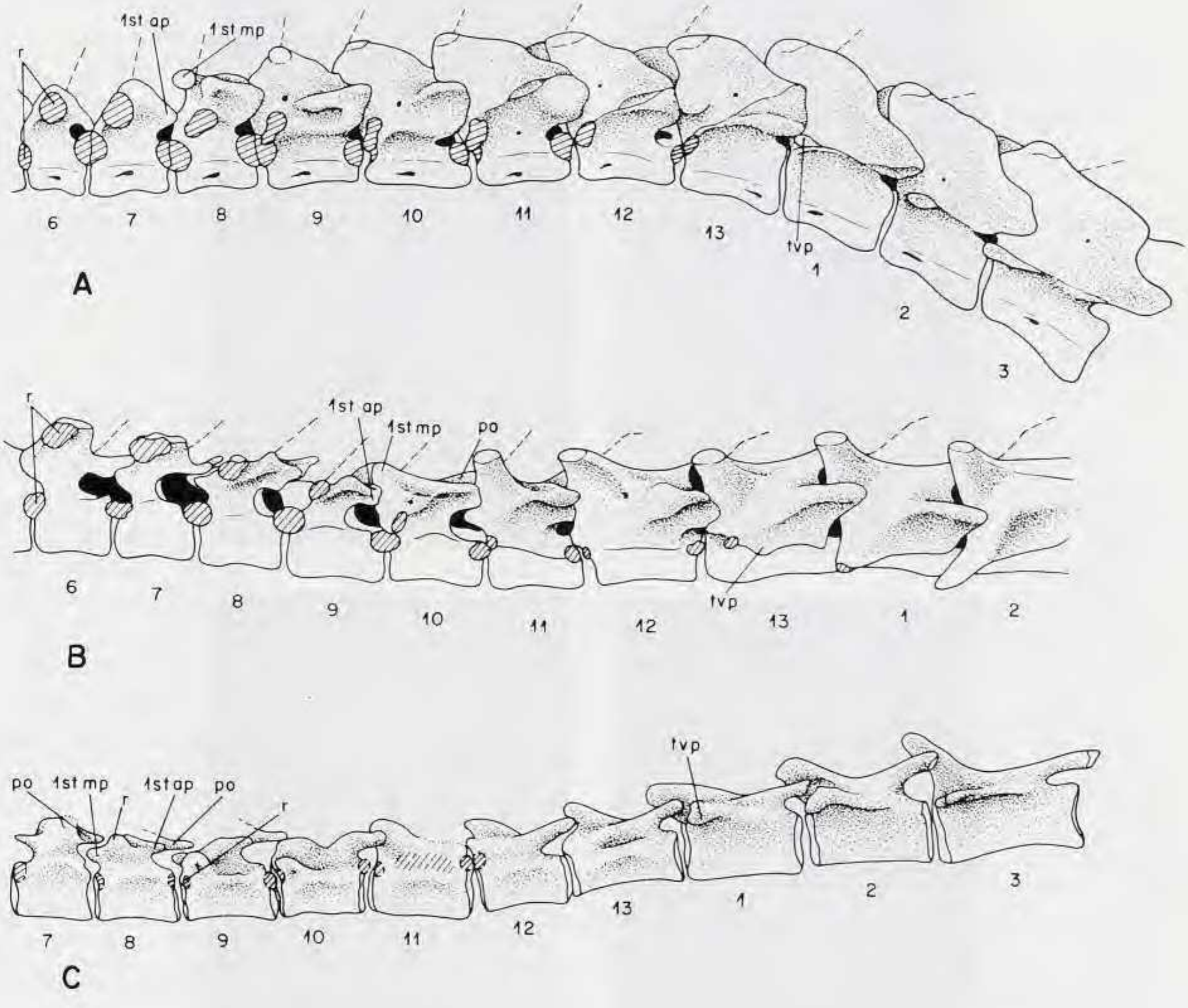


FIG. 30. — Schematic representation of thoracic and anterior lumbar vertebrae, in ventrolateral view (anterior is to left): A, *Didelphis* (MNHN A 3293 III 545), T6 to L3; B, *Metachirus nudicaudatus* (MNHN 1988-68), T6 to L2; C, *Pucadelphys andinus* (6106), T7 to L3. X 5/8. Abbreviations: **ap**, anapophysis; **mp**, metapophysis; **po**, postzygapophysis; **r**, rib attachment; **tvp**, transverse process. The dots indicate the direction of the neural spines.

FIG. 30. — Représentation schématique des vertèbres thoraciques et lombaires antérieures, en vue ventro-latérale (l'avant est à gauche): A, Didelphis *(MNHN A 3293 III 545), T6 à L3; B,* Metachirus nudicaudatus *(MNHN 1988-68), T6 à L2; C,* Pucadelphys andinus *(6106), T7 à L3. X 5/8. Abréviations:* ***ap****, anapophyse;* ***mp****, métapophyse;* ***po****, postzygapophyse;* ***r****, point d'attache des côtes;* ***tvp****, processus transverse. Les pointillés indiquent la direction des épines neurales.*

The ventral surface of the S1 vertebral body is almost flat; the sacral ribs (Fig.32, s r) flare anterolaterally, and the ends bend sharply ventrally with the lowest point at about mid-length. S2 is gently transversely convex. The transverse process of S1 flares anterolaterally and fuses with a posterior extension of the S2 transverse process, thus closing laterally the sacral foramen (s f).

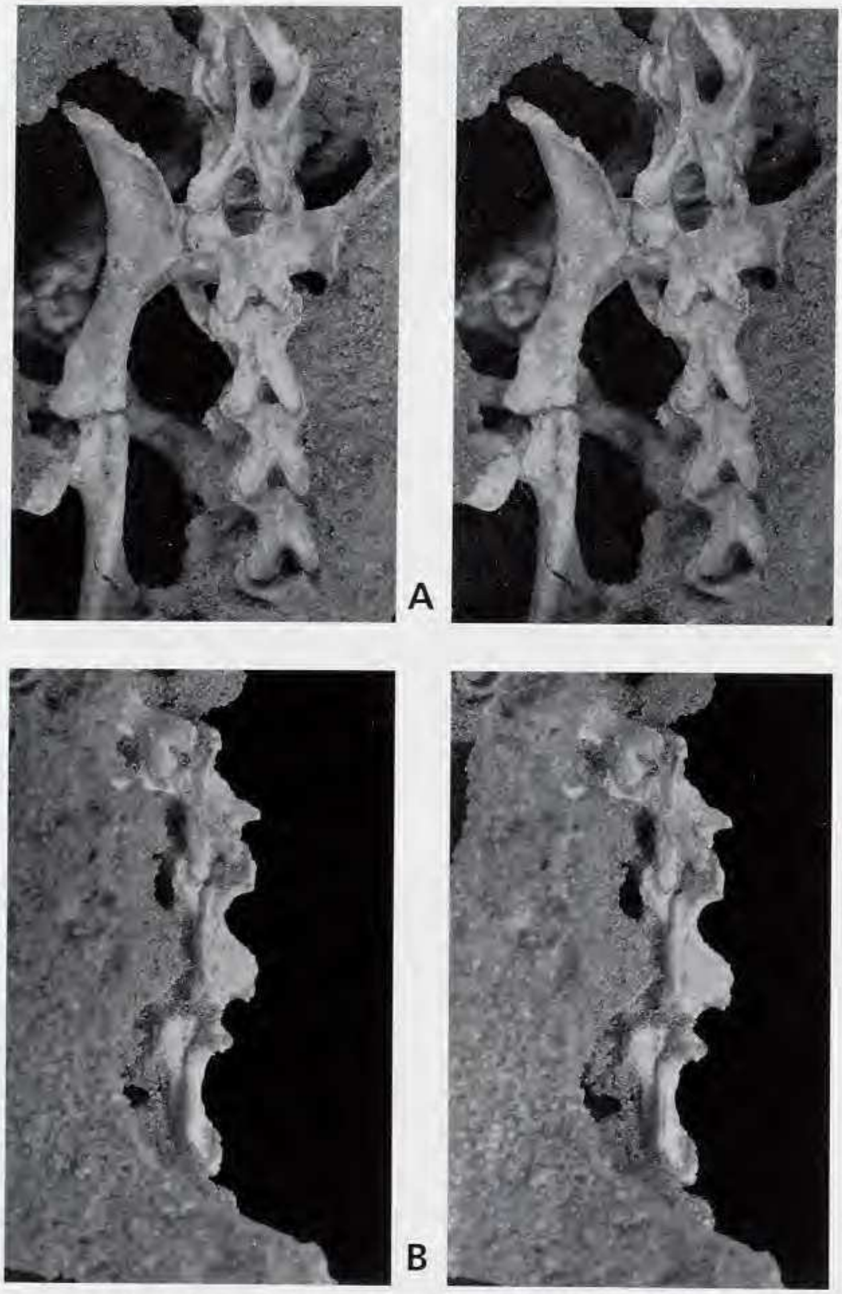


FIG. 31. — *Pucadelphys andinus*. Stereophotos. A, 6106, vertebrae L6-S1-S2, C1-C2 and left side of pelvis, dorsal view. X 3; B, 6106, vertebrae C4-C7, dorsal view. X 3.

FIG. 31. — Pucadelphys andinus. *Stéréophotos. A, 6106, vertèbres L6-S1-S2, C1-C2 et côté gauche du bassin, vue dorsale. X 3; B, 6106, vertèbres C4-C7, vue dorsale. X 3.*

The latter is subcircular, surrounded anteriorly and laterally by S1, and posteriorly by S2. Two nutrient foramina occur on the ventral body surfaces of S1 and S2. The ilio-sacral angle is estimated to have been around 15°.

Dorsally on Sl, the prezygapophyses are expanded as two widely separated wings; on S2 they are smaller, slightly closer to each other and, above all, not so ventrally flared. Still dorsally and behind the prezygapophyses, the base of the Sl transverse process is marked by a thick ridge, almost a step, oblique anterolaterally; lateral to it flares the thin sacral rib.

The base of the neural spine is preserved on S1 and S2; on S1 it extends along nearly the entire length of the arch, with the main part located at the posterior end; the spine was probably of moderate height and directed dorsally. On S2 the spine is very reduced and situated at the extreme posterior end only. On both S1 and S2 it is very thin transversely.

Caudal vertebrae (Figs 31, 33A and 34; Table 6a and b). — Represented in three specimens: 6106, C1 to C9, ventral view; 6110, C1 to C5, ventral view, C4 to C5, lateral view, C16?, ventral view, C17?, lateral, dorsal and ventral views, C20? and C21?, lateral, dorsal and ventral views; 6111, C1 to C9, dorsal view (C1 is fragmentary).

C1 to C5 are anterior caudals (*i.e.* those with zygapophyses), C6 is transitional, and C7 is the first posterior caudal. There were no haemal apophyses.

The lengths of the vertebral body on C1 to C4 are subequal in 6106 (and are all shorter than S2); beginning with C5 there is a notable elongation. Ventrally the vertebral body of C1 to C3 has a broad median longitudinal sulcus bounded laterally by low broad ridges; C4 and C5 have a low broad median ridge which flares posteriorly (on C5 it is more rounded); the longitudinal median ridge becomes narrower on C6 and C7, and more elevated on C8 and C9. The anterior and posterior epiphyses remain distinct ventrally and dorsally.

The neural spine of C1 (6106) is very short and narrow, located at the posterior end of the arch, and directed posterodorsally; on C2 none is detectable; C3 is not visible; there is apparently no spine on C4 and C5; from C6 to C9 the fused zygapophyses form a very low but long keel. Pre- and postzygapophyses are functional on C1 to C5, and prezygapophyses only on C6; they remain oblique; C7 has only tubercles that do not contact the preceding vertebra; ana- and metapophyses persist and interlock until C5 or C6.

The transverse processes (Figs. 31, 33 t p) on C1 to C3 are broad, situated at mid-length of the body, and are nearly perpendicular to the latter; on C4 and C5 they arise posteriorly on the body and flare posterolaterally; on C6 the body is narrow anteriorly and the transverse processes are broad and "wing-like" along the posterior part of the body; on C7 these posterior transverse processes are reduced, and there appear narrower, posterolaterally directed, anterior transverse processes; on C8 and C9, these anterior components have the lateral edges bent ventrally and they are slightly broader than the posterior components, which are reduced to lateral expansions.

The vertebral body of C16? to C21? consists of an elongate rod with greatly reduced anterior and posterior transverse processes; it decreases in width (but not length) from C16 to C21.

Discussion

Comparisons with *Eozostrodon-Megazostrodon, Henkelotherium, Asioryctes* and *Barunlestes* are based, respectively, on the works of Jenkins & Parrington (1976), Krebs (1991), and Kielan-Jaworowska (1977, 1978). These taxa were chosen as out-group comparisons.

Among living didelphids, comparison was made principally with *Metachirus nudicaudatus* (subadult, last molar not fully erupted, Laboratoire de Zoologie, Mammifères et Oiseaux, MNHN, specimen no 1988-68), *Monodelphis domestica*, *Philander opossum*, *Didelphis virginiana* (old adult) and *Perameles nasuta* (this taxon is used because it shares numerous specializations of the pelvic region with *Pucadelphys* as will be demonstrated below) (specimens from the collections in the Laboratoire d'Anatomie Comparée, MNHN, Paris, nos. 1967-330, A 3307, 1900-182 and

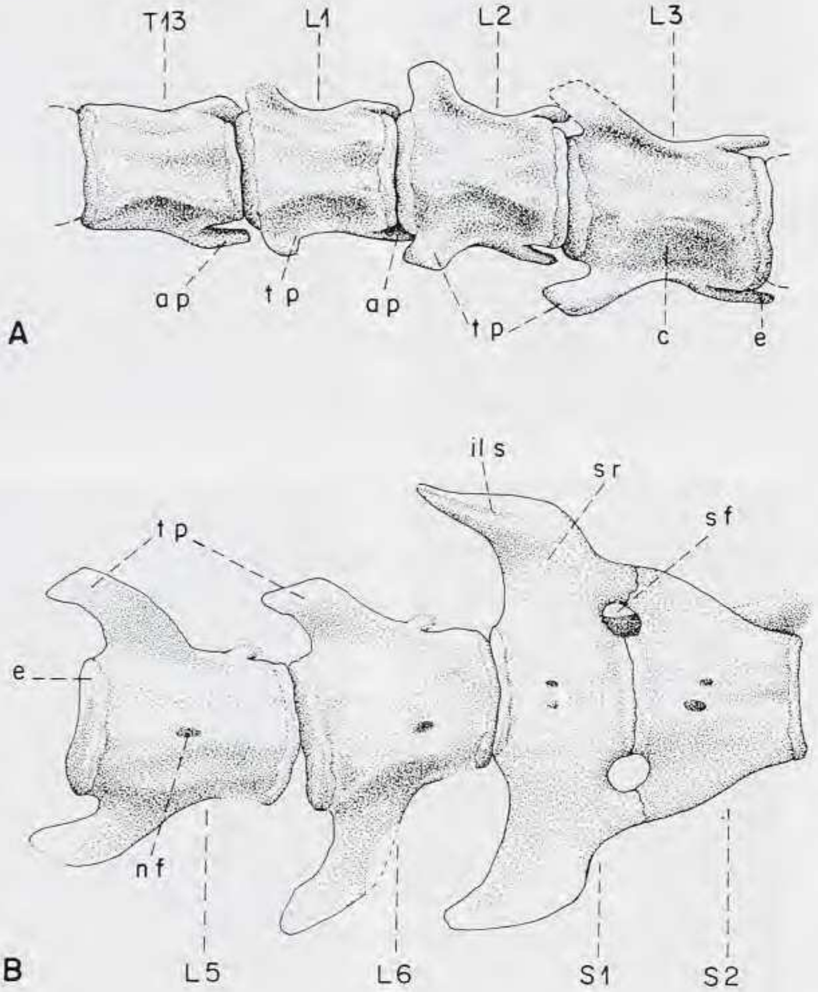


FIG. 32. — *Pucadelphys andinus*. 6106, thoracic, lumbar and sacral vertebrae: A, T13 and L1-3 (ventral face); B, L5-6, and S1-2 (ventral face). X 5. All drawn as preserved. Abbreviations: **ap**, anapophysis; **c**, centrum; **e**, epiphysis; **il s**, iliac surface; **n f**, nutrient foramen; **s f**, sacral foramen; **s r**, sacral rib; **t p**, transverse process.

FIG. 32. — Pucadelphys andinus. *6106, vertèbres thoraciques, lombaires et sacrées: A, T13 et L1-3 (face ventrale); B, L5-6, et S1-2 (face ventrale). X 5. Dessin en l'état de conservation. Abréviations:* ***ap****, anapophyse;* ***c****, centrum;* ***e****, épiphyse;* ***il s****, surface iliaque;* ***n f****, foramen nourricier;* ***s f****, foramen sacré;* ***s r****, côte sacrée;* ***t p****, processus transverse.*

1880-1020, respectively); special emphasis was laid on *Metachirus* because this taxon is one of, if not the, most primitive extant member of this group (REIG *et al.*,1987). For these comparisons, the works by COUES (1872), SLIPJER (1946) and TATE (1933) were also used.

The first point to be noted is the vertebral formula: *Pucadelphys* has 7 cervicals, 13 thoracics, 6 lumbars, 2 sacrals and ± 30 caudals, which is similar to that of many living didelphids (*e.g. Didelphis, Metachirus, Philander*).

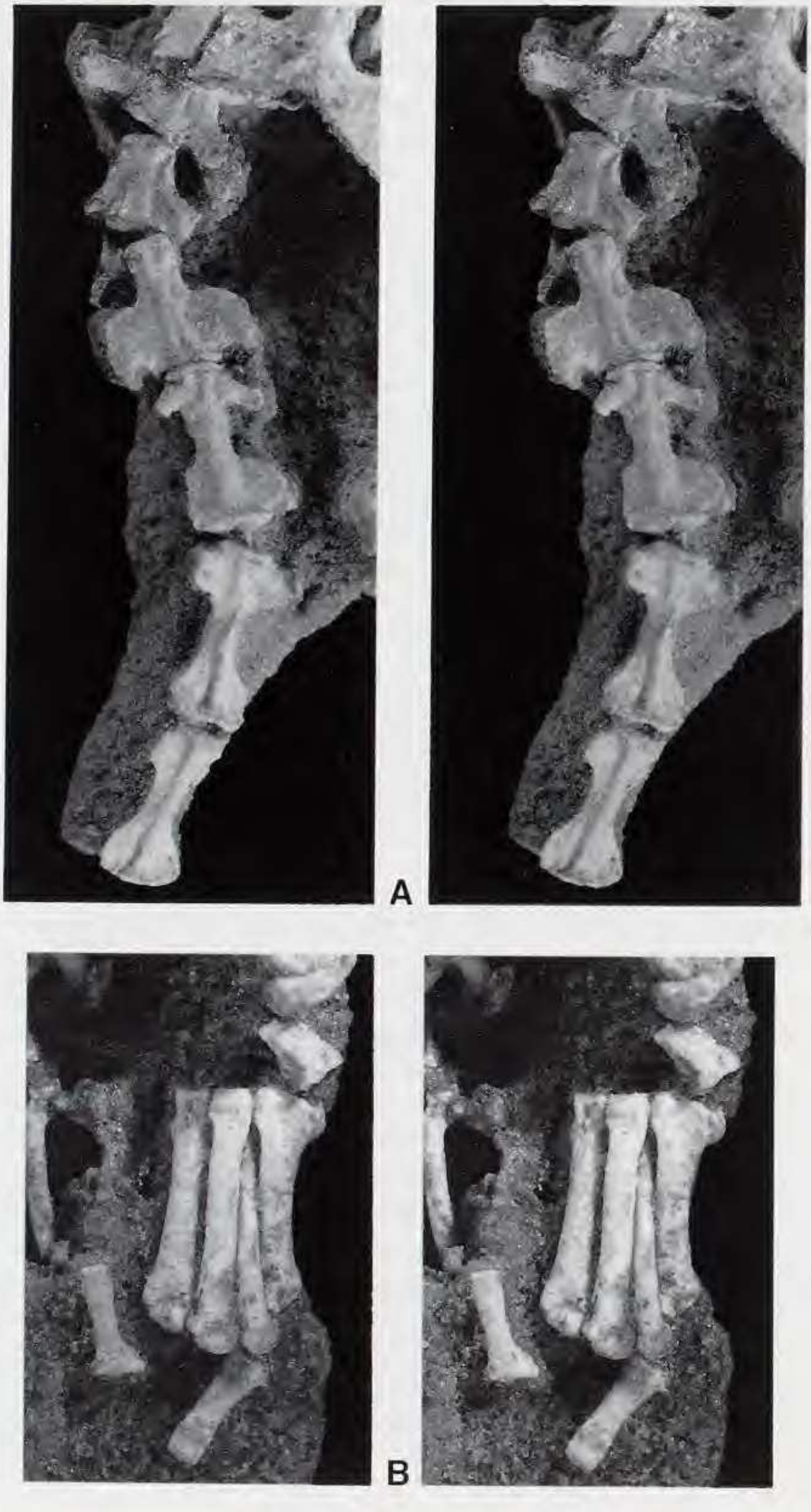
Atlas. — No atlas is preserved in *Henkelotherium*. Sutural linkage of the ossified intercentrum with the atlantal arch, as suggested in the above description of *Pucadelphys*, was also observed in *Barunlestes*, but not *Asioryctes* or *Eozostrodon*. A persisting suture between these two components makes the atlas of *Pucadelphys* less derived than in *Metachirus*, *Monodelphis* and *Didelphis*, where synostosis is complete. The presence of a fully enclosed transverse canal (though very narrow) is recorded in *Barunlestes* and considered as a derived state; this canal is not present in *Asioryctes*, *Didelphis*, *Monodelphis* or *Metachirus* (which means that the arteria vertebralis ran in a groove at the base of the transverse process); it thus seems doubtful that the tiny canal mentioned in *Pucadelphys* 6110 (Fig. 28, t c?) is homologous with the transverse canal, since the arterial sulcus is clearly visible at the base of the transverse apophysis; besides, a tiny canal similar to that in *Pucadelphys* is recorded in *Caenolestes* by OSGOOD (1921), who does not consider it as homologous to the transverse canal. On the other hand, the non closure of the canal for cranial nerve I as described in *Pucadelphys* is known only in three living marsupial genera (*i.e. Perameles*, *Marmosa* and *Monodelphis*). Other similarities with *Monodelphis* and *Metachirus* include the shallowness of the concavity of the axial facet and the shape of the transverse process.

In conclusion, only one character of the atlas of *Pucadelphys* (persisting suture between ossified intercentrum and atlantal arch) is more primitive than in the atlas of the living non-specialized didelphids.

Axis. — No axis is preserved in *Henkelotherium*. The large intervertebral space (between atlas and axis) observed in *Pucadelphys* was also recorded in *Eozostrodon* and, based on the regular anterior concavity of the axis, was probably present in *Asioryctes* and *Barunlestes*. Among the examined didelphids, this space is longest in *Didelphis*, where the axis is very specialized anteriorly (*i.e.* the spinous process is very deep with a ventrally protracted anteroventral edge).

The suture visible between the atlantal and axial components of the axis body (less accentuated in the adult 6105 than in the subadult 6110) is typical of primitive mammals as well as living adult marsupials: it is discernible in *Metachirus* (but only faintly visible in *Perameles*, *Monodelphis* and *Didelphis*) and is also recorded in *Zalambdalestes* and *Asioryctes*. The axial part is shorter than the atlantal part (dens excluded) in these last two genera; it is longer in *Metachirus*, *Monodelphis*, *Perameles* and *Didelphis*, as in *Pucadelphys*.

The axis spine of *Pucadelphys* is not as specialized as in *Asioryctes* or *Zalambdalestes*. It is also not as specialized as in *Didelphis* or *Perameles*, but is very similar to that of *Metachirus* and *Monodelphis*; as already mentioned, the anterior border of the axial arch in *Pucadelphys* is indeed more similar in shape and orientation to that of *Metachirus* than to that of *Didelphis*, where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B

it is more sharply inclined ventrally. As for the posterior border, it slightly contacts the arch of CV3 as in *Metachirus* and *Monodelphis*, but not *Philander*.

The two roots of the transverse process, separated in *Pucadelphys*, are united in the living marsupials as well as in *Zalambdalestes*; thus, the absence of a transverse canal in *Pucadelphys* represents the plesiomorphic state. Finally, an unfused axial rib may have been present in *Pucadelphys*: among living marsupials a freely articulating cervical rib is only reported in *Perameles* (GRASSÉ, 1967: 608), *Caenolestes* and *Phascogale* (OSGOOD, 1921).

In conclusion, the axis shows two characters (absence of transverse canal -only the sulcus is present-, unfused axial rib) less derived than in generalized living didelphids.

Cervicals 3-7. — The epiphyses of the cervical vertebral bodies are not distinct in *Henkelotherium* or *Eozostrodon*, but remain so in *Pucadelphys* (and in the examined marsupials except *Didelphis*). In contrast, the neural-centrum suture is open in *Henkelotherium* but not in *Pucadelphys*. The shape of the vertebral body of the latter is similar to that of *Metachirus*. The neural spines are rod-like in *Eozostrodon*, low in *Henkelotherium* and *Metachirus*, almost non existant in *Perameles*, *Monodelphis* and *Philander* (at least until CV5) but high in *Didelphis* where they synostose with each other (a specialization of that genus); they were reduced to tubercles in *Asioryctes* and zalambdalestids, and apparently low and separated in *Pucadelphys*.

An enclosed transverse canal is present in CV3-CV6 of *Pucadelphys*, but absent on CV7 as in zalambdalestids, *Metachirus*, some specimens of *Caenolestes* and several other marsupials (e.g. *Perameles)*; this again represents the plesiomorphic state. There were no cervical ribs other than axial in *Pucadelphys* (nor in *Henkelotherium*, but possibly some in *Eozostrodon*).

The presence of an inferior lamella on CV6 is typical of all therians known in that respect, including *Asioryctes* and *Barunlestes*; the situation is not known in *Henkelotherium*.

In conclusion, the cervical vertebrae in *Pucadelphys* resemble those of living generalized didelphids.

In summary, primitive characters of the cervical vertebrae of *Pucadelphys* (i.e. absence of a transverse canal on atlas, axis and CV7, possible axial rib, shape of the axis arch) are not collectively found in any of the living didelphids examined.

Thoracic vertebrae. — In *Henkelotherium* the number of thoracics and even presacrals is not known, and no certain thoracic vertebra is preserved.

The number of thoracics in *Pucadelphys* (13) is the same as in living didelphids and *Perameles*. T8-T9 are transitional vertebrae in *Pucadelphys* (Fig. 30C) and *Monodelphis*, T7-8 in *Didelphis* (Fig. 30A), T9 in *Philander* and T9-10 in *Metachirus* (Fig. 30B).

FIG. 33. — *Pucadelphys andinus*. Stereophotos. A, 6106, vertebrae C4 to C9, ventral view. X 3; B, 6105, left partial pes, dorsal view. X 3.

FIG. 33. — Pucadelphys andinus. *Stéréophotos. A, 6106, vertèbres C4-C9, vue ventrale. X 3; B, 6105, pied gauche partiel, vue dorsale. X 3.*

Source : MNHN, Paris

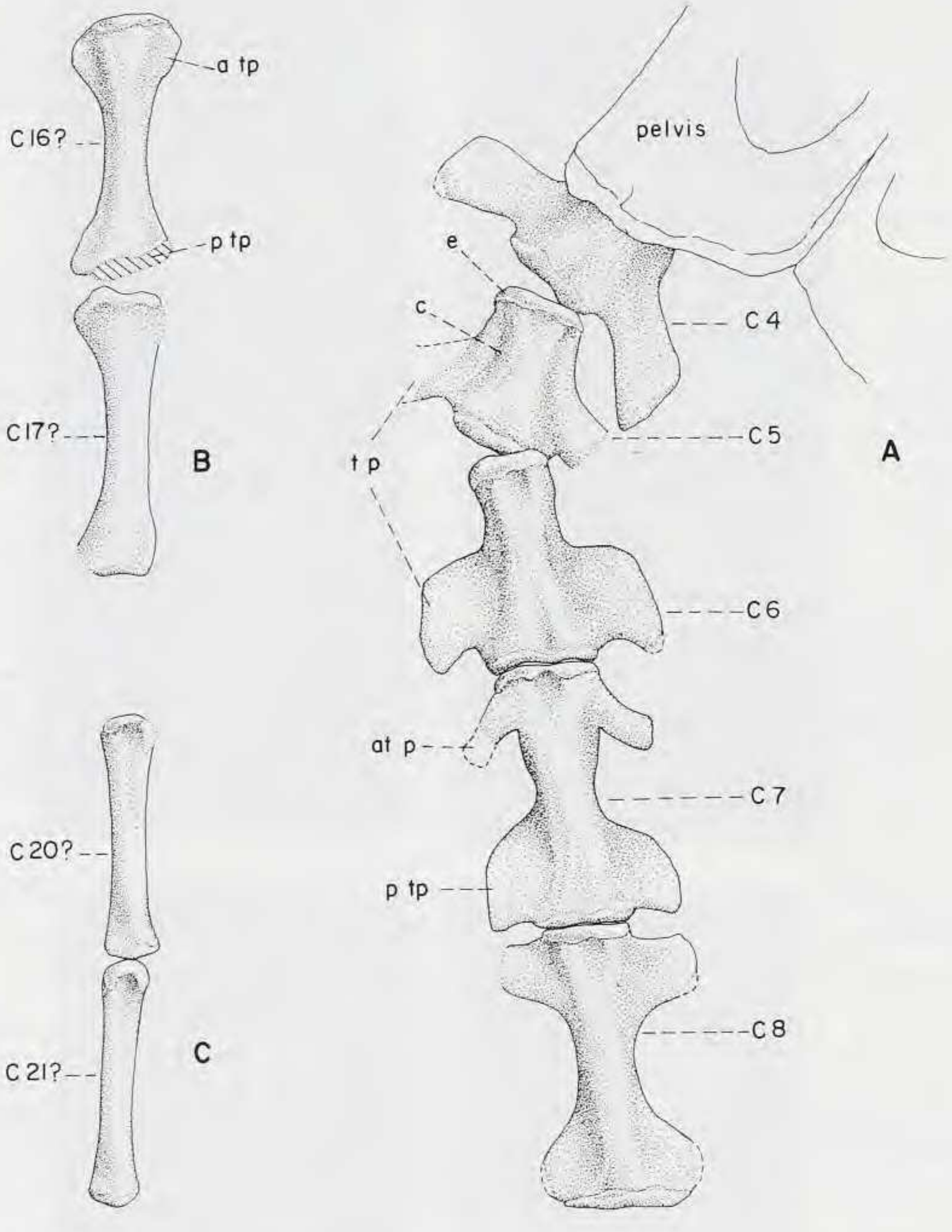


FIG. 34. — *Pucadelphys andinus.* Caudal vertebrae: A, 6106, C4 to 8, ventral face; B, 6110, C17?, C18?, C20? and C21?, ventral face. X 5. All drawn as preserved. Abbreviations: **at p**, anterior transverse process; **e**, epiphysis; **c**, centrum; **t p**, transverse process; **p tp**, posterior transverse process.

FIG. 34. — Pucadelphys andinus. *Vertèbres caudales: A, 6106, C4-C8, face ventrale; B, 6110, C17?, C18?, C20?, et C21?, face ventrale. X 5. Dessins en l'état de conservation. Abréviations;* ***at p****, processus transverse antérieur;* ***e****, épiphyse;* ***c****, centrum;* ***t p****; processus transverse;* ***t p****, processus transverse postérieur.*

In *Asioryctes* (only the first thoracic is preserved) and *Barunlestes* (the last three preserved), the transverse processes are short; there is no spine, only a tubercle; the vertebral body is wider than long; and accessory processes (meta- and anapophyses) are also present.

In *Didelphis, Perameles* and *Metachirus*, the thoracic spines, longer in the anterior part of the series than in *Pucadelphys*, become short and stouter posteriorly; in *Monodelphis* and *Philander*, they are short and inclined more and more posteriorly, while in *Didelphis* they contact each other on the posterior vertebrae, a specialized state relative to that of the other genera. In *Pucadelphys*, there is no evidence of an anticlinal spine, no more than in living didelphids, but in *Perameles* the spinal orientation reverses at T11. Finally, in *Pucadelphys, Metachirus* and *Perameles*, the epiphyses are distinct, whereas they are hardly so in *Didelphis* or *Monodelphis*.

In conclusion, the thoracic series in *Pucadelphys*, though not completely preserved, is comparable to that of the living didelphids.

Lumbar vertebrae. — The number of lumbars is not known for certain in *Henkelotherium*, but is estimated to be at least six; there were possibly seven in *Barunlestes*, and there are six in living didelphids as in *Pucadelphys*. In *Pucadelphys, Metachirus, Monodelphis* and *Perameles*, as in *Barunlestes*, the lumbars show a lengthening of the body more posteriorly in the series than in *Henkelotherium, Philander* or *Didelphis*. The epiphyses are distinct in the latter genera, not by a suture, but by a thickening of the ends; they remain distinct by a suture in *Pucadelphys, Metachirus* and *Perameles*.

In *Pucadelphys*, the lumbar spinous processes are narrow, high and dorsally or anteriorly directed as in *Perameles*; in *Metachirus*, they are long, low and posteriorly oriented in the anterior lumbars, then they become higher, straight and finally slightly anteriorly directed; this arrangement is intermediate between that in *Pucadelphys* on the one hand, and that in *Didelphis* or *Philander* in the other, where they are all low and posteriorly directed except on L6; the same is true of *Monodelphis*, but the spines are even lower. The latter were long and low in *Barunlestes*, at least on L3. In *Henkelotherium* the spinous processes are not preserved.

Accessory processes are recorded on the lumbars of *Eozostrodon*; in *Henkelotherium* the anapophyses seem to be well developed; in *Metachirus* and *Pucadelphys* they are better developed than on the thoracics. They remain discrete in *Monodelphis*, where only metapophyses are developed, but they are stout in *Didelphis*. Their development seems to be related to a reduction of lateral flexion.

The short transverse processes of the lumbars of *Henkelotherium* do not seem to show an elongation towards the sacrum. They are also short in *Barunlestes* "as in *Didelphis*" (KIELAN-JAWOROWSKA, 1977); those of *Metachirus* and *Pucadelphys* form a very similar gradual series, being anterolaterally directed (as in *Perameles*), while those of *Philander* and *Monodelphis* are more discrete and those of *Didelphis* are more robust and form a more rigid ensemble.

In conclusion, the lumbar vertebrae of *Pucadelphys* form a rather specialized series (within didelphids at least), with a gradual lengthening of the body and transverse processes, and long neural spines anteriorly directed; this situation is comparable to that of *Perameles*.

Sacral vertebrae. — The sacrum is relatively much longer in *Barunlestes* than in *Pucadelphys*, due principally to elongation of S2. But in both genera, it is made of two vertebrae and there is only one fulcral vertebra. According to KIELAN-JAWOROWSKA (1978) this situation is primitive for Eutherians (the mean number of sacral vertebrae being 3). However, Lessertisseur & Saban (*in* GRASSÉ, 1967: 624) state: "le nombre total de vertèbres soudées en un sacrum est variable et ne permet guère d'envisager une ligne claire d'évolution". Besides, *Henkelotherium* has two true sacrals (with two robust sacral ribs), *Eozostrodon* two to three; in addition, cynodonts commonly had four to five (JENKINS, 1971), the Early Cretaceous triconodont *Gobiconodon* probably had three (JENKINS & SCHAFF, 1988) and monotremes do have three. This would seem to contradict KIELAN-JAWOROWSKA's statement. Among didelphids, the sacrum is made of two vertebrae; but whereas the two are almost equally apposed to the ilium in *Monodelphis* and *Didelphis*, there is only one and a half in *Philander* and only one in *Metachirus* (which incidentally covers less than 50% of the auricular surface of the ilium as opposed to more than 50% in *Pucadelphys*); moreover in *Metachirus*, S2, which has even a smaller contact with S1 than in *Pucadelphys*, has short transverse processes, shorter even than those of C1: clearly, in this taxon considered as primitive on other grounds, there is practically no differenciation of S2 towards a sacral status. But *Perameles*, which shows numerous specializations in that area, has the same sacral structure as *Metachirus* and *Pucadelphys*, with an even smaller auricular surface.

To conclude, if our interpretation of the lumbar vertebrae of *Pucadelphys* as derived is correct, it would seem coherent to consider its configuration of the sacrum as also derived, at least within didelphids.

Caudal vertebrae. — Comparison of the four distal caudals of 6110 with *Metachirus* indicates that they apparently correspond to C16? + C17?, and C20? + C21?. Assuming that the subsequent caudals were similar to those of the living didelphids (see below), the number of caudals for *Pucadelphys* is estimated to be about 30. The number in some living didelphids is as follows: *Monodelphis*, 18?; *Didelphis*, 26 to 29; *Chironectes*, 29 (FLOWER, 1885); *Philander*, 32; and *Metachirus*, 32. Also, *Pucadelphys* resembles *Monodelphis* and *Didelphis* in having 5 anterior caudals, a transitional C6, and the posterior caudals begin with C7; in *Metachirus* C5 is transitional while in *Philander* it is C4.

In *Didelphis*, the caudal vertebrae have specializations associated with a prehensile tail (KRAUSE & JENKINS, 1983: 242): e.g. tail long, commonly twice or more the length of the precaudal vertebral column; a median sulcus for abductor muscles and tendons crosses ventrally all the vertebrae, zygapophyses are more vertical, transverse processes are broad and robust for muscle attachments and present even in most distal caudals; moreover, haemal apophyses, that enclose abductor tendons and muscles, are large and developed along nearly entire length of tail; finally, sacral spinous processes are relatively well developed, commonly subequal to the height of the spinous processes of posterior lumbar vertebrae. No such specializations except high sacral spinous processes and a very slight ventral sulcus on caudals exist in *Philander* and *Metachirus*, haemal apophyses in *Monodelphis*; none of them were found in *Pucadelphys*. The caudal vertebrae of *Henkelotherium* also show prehensile specializations: haemapophyses, ventral sulcus, and mostly considerable elongation from C6.

The "evolution" of the caudal transverse processes observed along the tail is different in the examined didelphids: in *Didelphis* and *Monodelphis* the long transverse lamina divides into an anterior and a posterior component persisting together for a distance; in *Metachirus* the wide transverse process also divides, but the posterior component practically disappears on the vertebra following this division; in *Pucadelphys*, the situation is more complex than in this genus (see p. 109). As stated above, the transitional vertebra is C6 in *Pucadelphys, Didelphis, Monodelphis* and *Caenolestes*, and C5 in *Metachirus*.

Spinous processes are totally absent on the caudals of *Caenolestes* and *Monodelphis*, very faint in *Metachirus* and *Didelphis*, high on anterior caudals in *Perameles*, while rather low in *Pucadelphys*.

In conclusion, there is no indication that the tail was prehensile in *Pucadelphys*.

APPENDICULAR SKELETON.

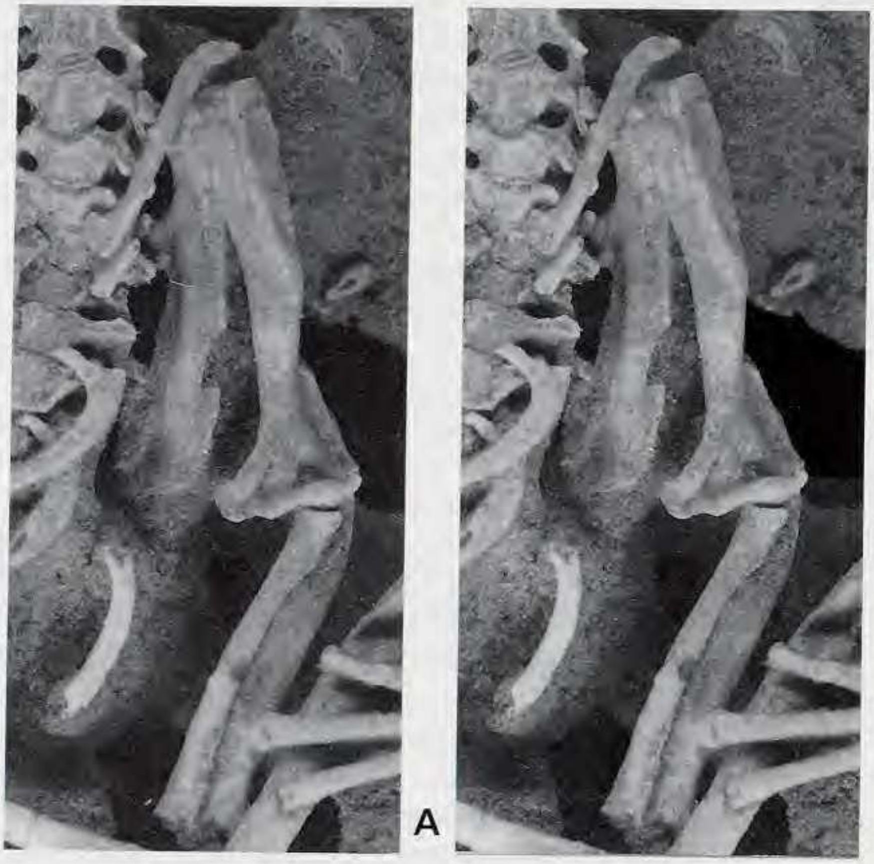
SHOULDER GIRDLE

Scapula (Figs 24B, 35B, 36 and 38A; Table 7). — Four elements: 6105, left, external and partial internal views; 6106, partial right, internal and external views - distal extremity of left, internal view; 6110, distal fragment of left, internal view; 6111, proximal fragment of left, external view.

Notable features are the straightness of the posterior border (Fig. 36, pb), the relative anteroposterior narrowness of the scapular plate (s p), the slight anteroposterior convexity of the internal face along the posterior border, the anteromedial protrusion of the large coracoid process (c), and the depth of the supracoracoid incisure (s i). The plate itself is very thin and the suprascapular border (s b) is not thickened. The spine (s), for which we have only partial views (the best being on 6105), is very thin, relatively high and probably deflected; it decreases in height proximally. The acromion (a) (as preserved only on 6106, right) is a thin triangular (apex directed posteriorly) plate-like process, set perpendicular on the anterior part of the spine and parallel to the scapular blade. Its anterior edge extends slightly beyond, but parallels, that of the glenoid cavity (g c); its anterior-most projection lies nearly dorsal to the tuber scapulae (t s). The supraspinous fossa (s f) seems to have been slightly wider than the infraspinous fossa (i f) (testifying to a robust supraspinous muscle which itself contributes to a good shoulder mobility (JENKINS & WEIJS, 1979: 408). The glenoid cavity is ovoid in shape, very shallow, and the tuber scapulae high but not prominent (for insertion of the coraco-humeral ligament). The margin of the glenoid fossa is only slightly thickened. What may be the scapulocoracoid suture is visible only in 6106 (left).

Clavicle (Figs 25B, 26B, 35A, 37A and 38; Table 8). — Three elements: 6105, nearly complete left, anterior view - sternal extremity of right, posterior view; 6110, almost complete right, posterior view - incomplete left, anterior and dorsal views.

The clavicle has the form of a very elongate S. The scapular extremity (Fig. 37, sc e) is slightly oblong and was probably thickened, but it is flattened as preserved; the sternal extremity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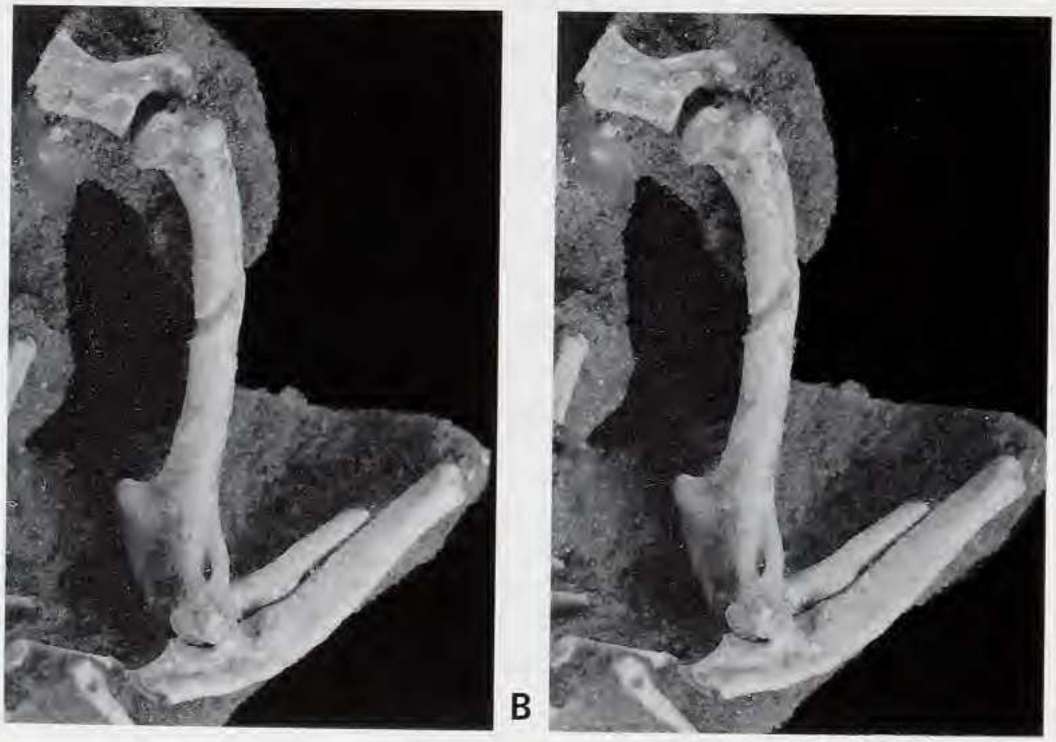
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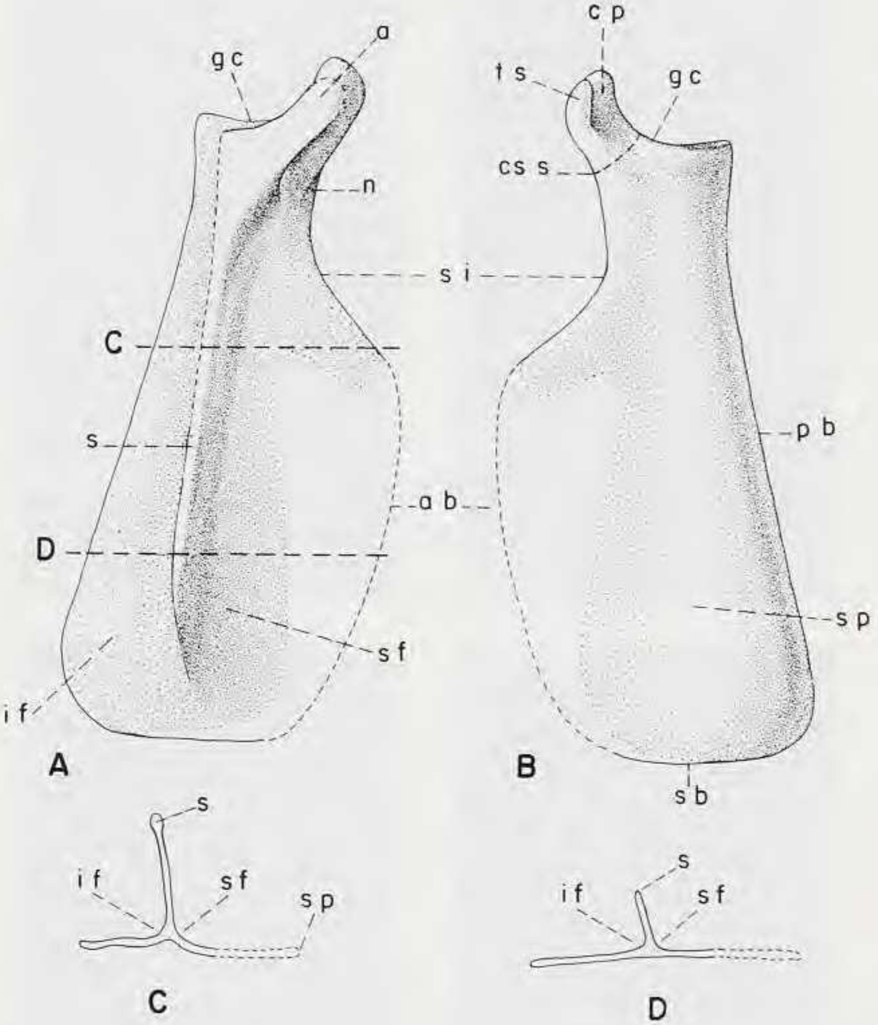


FIG. 36. — *Pucadelphys andinus*. Left scapula, reconstructed (6105 and 6106 combined): A, external face; B, internal face; C, anterior transverse section; D, posterior transverse section, X 5. Abbreviations: **a**, acromion; **a b**, anterior border; **c p**, coracoid process; **cs s**, coraco-scapular suture; **g c**, glenoid cavity; **i f**, infraspinous fossa; **n**, neck; **p b**, posterior border; **s**, spine: **s b**, suprascapular border; **s f**, supraspinous fossa; **s i**, suprascapular incisure; **s p**, scapular plate; **t s**, tuber scapulae.

FIG. 36. — Pucadelphys andinus. *Omoplate gauche reconstituée (basée sur 6105 et 6106): A, face externe; B, face interne; C, section transversale antérieure; D, section transversale postérieure. X 5. Abréviations: **a**, acromion; **a b**, bord antérieur: **c p**, processus coracoïdien; **cs s**, suture coraco-scapulaire; **g c**, cavité glénoïde; **i f**, fosse sous-épineuse; **n**, col; **p b**, bord postérieur; s, épine; **s b**, bord supra-scapulaire; **s f**, fosse sus-épineuse; **s i**, incisure suprascapulaire; **s p**, lame scapulaire; **t s**, tuber scapulae.*

FIG. 35. — *Pucadelphys andinus*. Stereophotos. A, 6105, left clavicle, scapula, humerus, ulna and radius, ventroposterior view. X 3; B, 6106, distal extremity of left scapula, humerus, ulna and radius, posterolateral view. X 3.

FIG. 35. — Pucadelphys andinus. *Stéréophotos. A, 6105, clavicule gauche, omoplate, humérus, cubitus et radius, vue ventro-postérieure. X 3; B, 6106, extrémité distale de l'omoplate gauche, humérus,cubitus et radius, vue postéro-latérale. X 3.*

(st e) is much flatter and expanded, concave anteriorly (for the omosternal cartilage linking it to the interclavicle) with a raised and thickened posterior border; it is situated at a right angle relative to the shaft; its posterior face is relatively flat. The anterior face of the shaft shows a spiral-like transverse convexity, while the posterior face is flatter.

Interclavicle (Figs 25B and 37B; Table 9). — Preserved only in 6105, very slightly distorted, ventral and partial dorsal views.

The interclavicle is well ossified and relatively long; the anterior process (which supports anteriorly the clavicle) and the posterior process (which supports the first rib laterally) are only slightly unequal in breadth, but the anterior part is shorter than the posterior one. Ventrally it bears a long and high keel which heightens distally, where the bone is as high as it is wide. The short triangular arms face laterally and terminate with a "costal tubercle" (Fig. 37, c t). A broad anteroposterior sulcus occurs at the base of the arms between the median ridge (m r) and costal tubercle. Dorsally the bone seems to have been slightly concave.

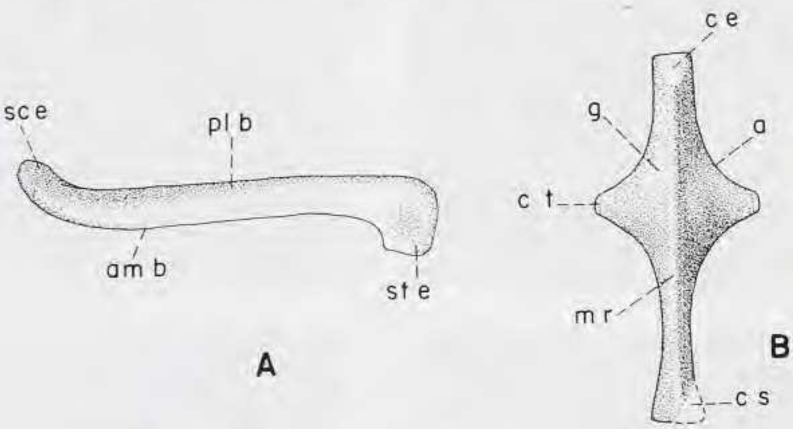


FIG. 37. — *Pucadelphys andinus*. 6105: A, left clavicle and B, interclavicle, ventral face. X 5. Drawn as preserved. Abbreviations: **a**, transverse arm; **am b**, anteromesial border; **c e**, cephalic extremity; **c s**, caudal surface; **c t**, costal tubercle; **g**, groove; **m r**, median ridge; **pl b**, posterolateral border; **sc e**, scapular extremity; **st e**, sternal extremity.

FIG. 37. — Pucadelphys andinus. *6105: A, clavicule gauche et B, interclavicule, face ventrale. X 5. Dessins en l'état de préservation. Abréviations:* ***a****; branche transversale;* ***am b****, bord antéro-mésial;* ***c e****; extrémité céphalique;* ***c s****, surface caudale;* ***c t****, tubercule costal;* ***g****, sillon;* ***m r****, côte médiane;* ***pl b****, bord postéro-latéral;* ***sc e****, extrémité scapulaire;* ***st e****, extrémité sternale.*

FORELIMB

Humerus (Figs 35, 38 and 39; Table 10). — Six elements: 6105, nearly complete left, anterior view - distal half of right, all views; 6106, most of right diaphysis, anterior view - complete left, posterointernal view; 6110, nearly complete right, posterior view - nearly complete left, internal view; 6111, distal half of left, posterointernal view - a small fragment of the distal end of the right.

The humerus is stout. The head (Fig. 39, h) covers about 50% of the width of the proximal end, and extends only slightly beyond the level of the tuberosities; it is transversely narrow and

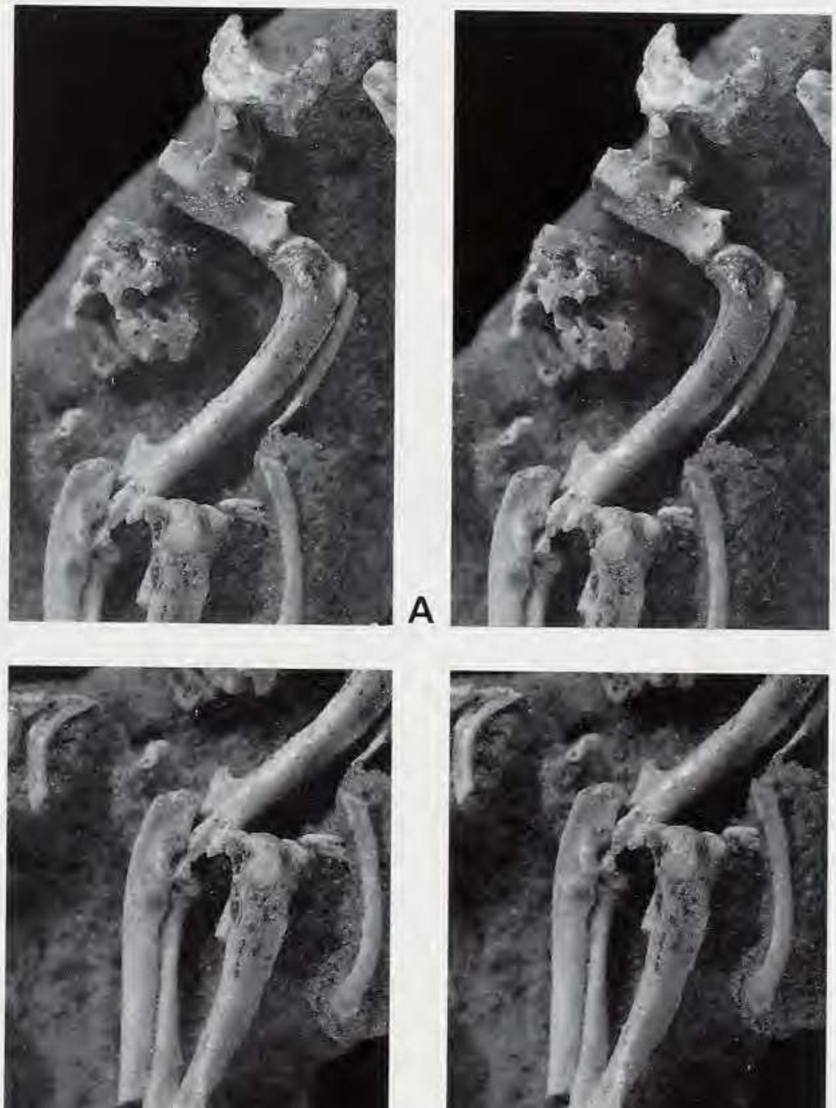


FIG. 38. — *Pucadelphys andinus*. Stereophotos. A, 6110, axis, left lateral view; fragments of left scapula and humerus, internal view; left clavicle, anterior view. X3; B, 6110, right humerus, posterior view, left ulna and radius, internal view; left clavicle, posterior view, X 3.

FIG. 38. — Pucadelphys andinus. *Stéréophotos. A, 6110, axis, vue latérale gauche; fragments d'omoplate gauche et d'humérus, vue interne; clavicule gauche, vue antérieure. X 3; B, 6110, humérus droit, vue postérieure; cubitus et radius gauches, vue interne; clavicule gauche, vue postérieure. X 3.*

curves sharply posteroventrally. The greater tuberosity (g t) is subequal in breadth, but is overall larger, than the lesser tuberosity (l t); it is separated from the head by a slight sulcus, and grades distally into a long deltopectoral crest (dp c) which extends half the length of the diaphysis. The large deltopectoral surface is triangular (apex points distally), planar, and somewhat turned down internally; it bears only small rugosities. The lesser or internal tuberosity is not sharply demarcated from the head (only a narrow sulcus is visible on the left side of 6106). A wide and deep bicipital groove (b g) separates the two tuberosities anteriorly and continues distally between the deltoid

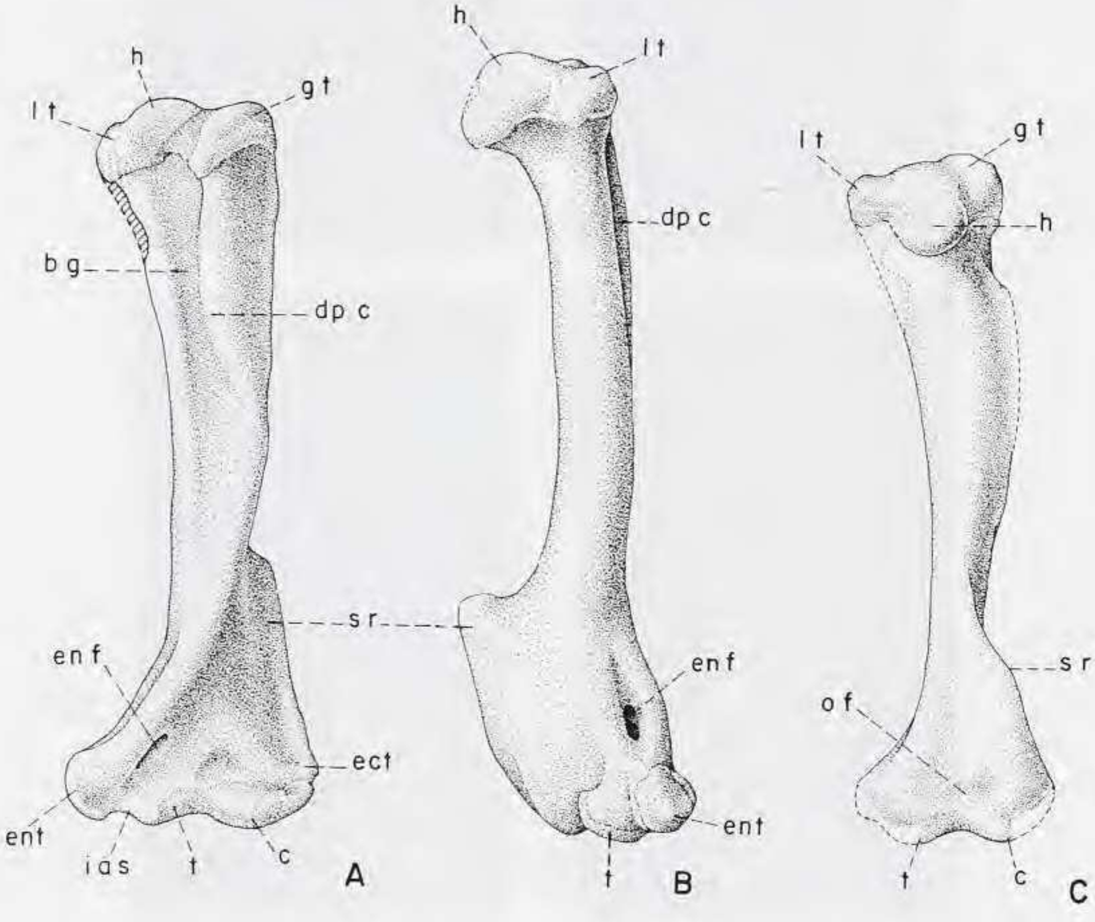


FIG. 39. — *Pucadelphys andinus*. Humerus: A, 6105, left, anterior face; B, 6106, left, posteromesial face; C, 6110, right, posterior face. X 5. All drawn as preserved. Abbreviations: **b g**, bicipital groove; **c**, capitulum; **dp c**, deltopectoral crest; **ect**, ectepicondyle; **ent**, entepicondyle; **en f**, entepicondylar foramen; **g t**, greater tuberosity; **h**, head; **i a s**, internal articular sulcus; **l t**, lesser tuberosity; **o f**, olecranon fossa; **s r**, supinator ridge; **t**, trochlea.

FIG. 39. — Pucadelphys andinus. *Humérus: A, 6105, gauche, face antérieure; B, 6106, gauche, face postéro-mésiale; C, 6110, droit, face postérieure. X 5. Dessins en l'état de conservation. Abréviations:* ***b g****, sillon bicipital;* ***c****, capitulum;* ***dp c****, crête delto-pectorale;* ***ect****, ectépicondyle;* ***ent****, entépicondyle;* ***en f****, foramen entépicondylien;* ***g t****, grande tubérosité;* ***h****, tête;* ***ias****, sillon articulaire interne;* ***l t****, petite tubérosité;* ***o f****, fosse olécranienne;* ***s r****, crête du supinateur;* ***t****, trochlée.*

crest and the posteroexternal border of the bone. Distal to the deltopectoral crest, the diaphysis is narrow, subcylindrical in cross-section; but the bone rapidly flattens anteroposteriorly and flares transversely; at that level, it is limited externally by a broad and thin supinator ridge (s r) that extends along about 30% of the diaphysis. Internally this expanded part is limited by the entepicondylar "crest" which consists of two ridges that border a pronounced sulcus, itself perforated by an elliptical entepicondylar foramen (en f); the anterointernal ridge ascends obliquely toward the deltopectoral crest. The suture between the proximal epiphysis and the diaphysis remains distinct in adults.

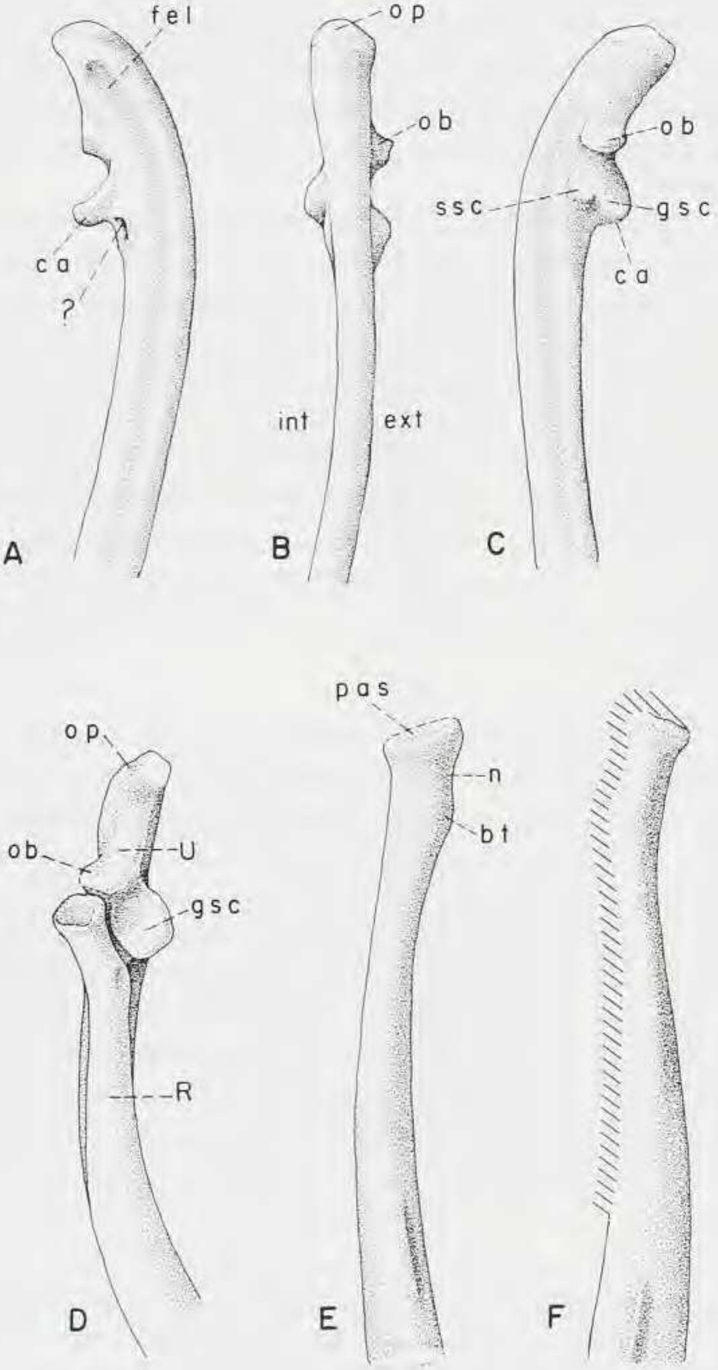
The distal end is transversely wide, but the articular surfaces are low and occupy only a narrow part of this width. The small ectepicondyle (ect) is not thickened anteroposteriorly; the entepicondyle (ent) is ovoid, slightly convex, and protrudes internally. External to it is a broad sulcus, sharply delimited posteriorly on its external side, less sharply anteriorly, and obliquely oriented (this is the internal articular sulcus of OSGOOD (1921), which in *Caenolestes* receives the inner upper lip of the sigmoid cavity of the ulna). The capitulum (c) is wide anteriorly; posteriorly it is reduced to a crest reaching the level of the base of the entepicondylar foramen. Anteriorly the trochlea (t) and capitulum grade into one another without delimitation; posteriorly and above the capitulum, the bone is depressed by a deep and short fossa which receives the olecranon during flexion of the forearm (o f). The measurements effected on the humerus of 6110 according to the method proposed by KIELAN-JAWOROWSKA & GAMBARYAN (1994) indicate that there was practically no twisting of the bone.

Ulna (Figs 35, 38B, 40A-D and 45C; Table 11). — Six elements: 6105, left, complete except for distal epiphyses, anteroexternal view - isolated proximal half of right, internal, external and posterior views; 6106, proximal half of left, internal view (olecranon incomplete); 6110, left, internal view - right proximal part, external view; 6111, median fragment of left diaphysis - isolated proximal half of right, anterointernal view.

In length, the ulna is equal to or slightly greater than the humerus. It is wider than the radius, hence stout. The olecranon process is long, with a convex upper border (6111 right); it is slightly inclined internally; there is no terminal tubercle. The anterior margin of the olecranon appears to be slightly concave. Its internal face is depressed by a longitudinal sulcus, while its external face is practically flat. The "beak" of the olecranon is directed externally, with no internal projection.

The greater sigmoid cavity (g s c) is narrow, high, oblique dorsoventrally and externointernally, convex transversely on the internal part for the humerus, and flat on the external part, also apparently for the humerus. The lesser sigmoid cavity (s s c) for the radius is apparently small and only slightly excavated. There is a well developed coronoid apophysis (c a), but there is no internal coronoid tubercle; this apophysis is strongly protruding internally, anteriorly underlain by a depression with an orifice, and limited laterally by a strong ridge. The diaphysis is very compressed laterally so as to form a ridge posteriorly; distally it becomes more ovoid, slightly arched and slightly narrower. No distal extremity is preserved; the most complete specimen (6105) did not have the distal epiphysis fused, and it was lost during fossilization.

Radius (Figs 35, 38B, 40D-F and 45C; Table 12). — 6105, left, complete except for distal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epiphysis, anteroexternal view - isolated, proximal half of right, anterior, external and internal views; 6106, left proximal third, internal view; 6110, left, internal view; 6111, fragment of left diaphysis - isolated proximal half of right, anterointernal view.

The anteroposterior curvature of the bone is gentle, the lateral one is more pronounced distally. The proximal articular surface (Fig. 40, p a s) is ovoid and compressed with a transverse long axis, and noticeably concave. Under the thickened proximal border, there follows a neck (n), itself immediately followed by a strong bicipital tuberosity (b t), rather highly situated. The anterior face of the bone is convex proximally, becomes flat distally, the anterior ridge quickly disappearing; the external face, wide proximally, becomes more convex distally, where a median sulcus is discernible, presumably for the ulnar crest; the internal face narrows to a ridge distally. The diaphysis is triangular in cross-section at mid-length. No distal extremity is preserved.

In each case, the ulna and radius are, as preserved, in contact along nearly their entire length: only under the bicipital tuberosity is there a very narrow interosseous space. This testifies to a very limited capacity of rotation. Proximally the bones are situated anteroposteriorly relative to each other, but soon torsion brings the radius in an internal position relative to the ulna.

Manus. — Nothing is unquestionably preserved of the hand, but see cautionary remarks under pes (p. 139).

Discussion

Scapula. — In *Megazostrodon*, there is no distinct supraspinous fossa. In *Henkelotherium*, the scapula remains more primitive than in *Pucadelphys* with a massive coracoid component, but the supraspinous fossa is said to cover almost two-thirds of the external surface.

No scapula is preserved in *Asioryctes*. In *Barunlestes*, where the ventral part is preserved, the extensive tuber scapulae and the coracoid process were developed in a way more reminiscent of metatherians than of modern claviculate eutherians. In *Pucadelphys*, the tuber scapulae is smaller than the coracoid process, as in *Metachirus*. In *Barunlestes*, the spine starts at about the same level as in *Pucadelphys*, that is, slightly higher than in *Didelphis*. In the latter, the two fossae are subequal (as in *Perameles*), the spine is thicker than in *Pucadelphys*, the posterior border more convex, the glenoid cavity flatter and more complex, and the internal face regularly concave; there is no overhang of the coracoid process, and the plate itself is relatively thicker.

In *Philander*, the infraspinous fossa remains very slightly larger than the supraspinous

FIG. 40. — *Pucadelphys andinus*. A-C, 6105, proximal part of right ulna: A, internal face; B, posterior face; C, external face. D, isolated, proximal end of articulated right ulna and radius, anterior view; E- F, proximal end of left radius: E, 6105, internal face: F, 6110, anteroexternal face. X 5. All drawn as preserved. Abbreviations: **b t**, bicipital tuberosity; **c a**, coronoid apophysis; **ext**, external; **f e l**, fossa for exterior ligament; **g s c**, greater sigmoid cavity; **int**, internal; **n**, neck; **o b**, olecranon beak; **o p**, olecranon process; **p a s**, proximal articular surface; **R**, radius; **s s c**, lesser sigmoid cavity; **U**, ulna.

FIG. 40. — Pucadelphys andinus. *A-C, 6105, partie proximale du cubitus droit: A, face interne; B, face postérieure; C, face externe; D, spécimen isolé, extrémité proximale du cubitus et du radius en articulation, vue antérieure; E-F, extrémité proximale du radius gauche: E, 6105, face interne; F, 6110, face antéro-externe. X 5. Dessins en l'état de conservation. Abréviations:* ***b t****, tubérosité bicipitale;* ***c a****, apophyse coronoïde;* **ext***, externe;* ***fe l****, fosse pour le ligament externe;* ***g s c****, grande cavité sigmoïde;* **int***, interne;* ***n****, col;* ***o b****, bec de l'olécrane;* ***o p****, processus olécranien;* ***p a s****, surface articulaire proximale;* ***R****, radius;* ***s s c****, petite cavité sigmoïde;* ***U****, cubitus.*

fossa; otherwise the bone is comparable to that of *Metachirus;* but in the latter as in *Monodelphis*, it is the supraspinous fossa which is slightly larger than the infraspinous, the spine is very thin, the posterior border straight, and the acromion not thickened, all character states as in *Pucadelphys*. However, in *Metachirus* the tuber scapulae is lower, and the coracoid process less recurved internally than in the other two genera; the coracoscapular suture remains distinct, at least in the subadult specimen which we used for comparisons. Finally, the scapula of *Monodelphis* has a deflected spine as in *Pucadelphys*.

It thus appears that *Pucadelphys* has an unspecialized scapula, combining all primitive character states found isolated in living didelphids.

Clavicle. — The assignment of this bone to *Eozostrodon* is only tentative. The clavicle of *Henkelotherium*, which must have been quite long, is rounder than that of *Pucadelphys* and not widened sternally. No clavicle is preserved in the Mongolian eutherians.

The clavicle of *Didelphis* shows the same general features as that of *Pucadelphys* (but the torsion is more accentuated relative at least to the preserved state in *Pucadelphys*, which may be the result of some flattening during fossilization) and the interclavicular extremity more flattened; also the scapular extremity does not make an angle on the long axis; finally it is relatively shorter (1/2 of length of the scapula, compared to 2/3 in *Pucadelphys*).

In *Metachirus*, the clavicle is not as clearly S-shaped as in *Pucadelphys*, and there is no posterior spiral convexity; but the sternal extremity is hollowed ventrally with a raised medial border as in *Pucadelphys*. The clavicle of *Monodelphis* is more similar to that of *Pucadelphys*, but its sternal extremity, though less angled relative to the shaft, is relatively wider; the same is true of *Metachirus*. In *Perameles*, the clavicle is absent or rudimentary.

In conclusion, the clavicle of *Pucadelphys* is that of a typical non specialized didelphid.

Interclavicle. — The homologies of this bone have been widely disputed; it seems logical to consider it as homologous to the episternum of monotremes and to the "manubrium" of *Caenolestes* (Osgood, 1921). No interclavicle is known in Cretaceous therians, and, according to Krebs (1991), none was developed in *Henkelotherium*. As for *Eozostrodon*, the same remarks noted for the clavicle apply to the interclavicle.

In *Didelphis*, the interclavicle is shorter than in *Pucadelphys* and the arms divide it longitudinally into two equal parts; it is also more concave dorsally, and the ventral keel completely disappears distally. Similarly in *Perameles*, this keel becomes considerably lower distally. In *Metachirus* the bone is very similar to that of *Pucadelphys*. In *Monodelphis*, the anterior and posterior parts are also quite unequal as in the latter two genera, but there is practically no ventral keel.

Overall, the interclavicle of *Pucadelphys* is typically didelphid.

Humerus. — In *Henkelotherium*, the bone is long and robust; a peculiarity is a strongly marked muscular insertion on the mesial face of the shaft not found in *Pucadelphys*, which presumably would represent the derived state for this character: in *Eozostrodon* the bump is even more accentuated than in *Henkelotherium*. Also in the latter, the deltoid crest is robust but relatively shorter (1/3 of the bone against 1/2 in *Pucadelphys*). The entepicondyle is prominent. Compared to *Barunlestes*, 6105 has a less curved diaphysis, the deltopectoral crest is more prominent; there is the same groove between both tuberosities. But most notable is the difference concerning the distal extremity, which is much wider in *Pucadelphys*; also the entepicondyle is better developed and there is no supratrochlear foramen; finally, the susepicondylian crest is lacking in *Barunlestes*, and the supinator ridge is not as wide and sharp.

In *Metachirus*, the bone is relatively more slender than in *Pucadelphys*, the deltopectoral surface is as smooth and long but not deflected as in *Pucadelphys*, and the supinator ridge is relatively shorter. There is no third distal articular surface; such a feature, described above in *Pucadelphys*, is mentioned by OSGOOD (1921) for *Caenolestes* as being exceptional for marsupials, and he considers it as more indicative of digging than cursorial habits. The humerus of *Didelphis* is more similar to that of *Pucadelphys* than to that of *Metachirus*: the proportions of the bone are slightly different and the head is relatively wider, but dorsally the latter does not extend beyond the tuberosities any more than in *Pucadelphys*; the deltopectoral ridge extends over half of the length of the bone and the deltopectoral surface is turned downward as in *Pucadelphys*; finally, a clear sulcus also separates the entepicondyle and trochlea, without however articulating with the upper lip of the ulna. The situation is the same in *Philander* and *Monodelphis*, whose humerus is very close to that of *Pucadelphys* in every aspect: proportions, triangular and deflected deltopectoral surface, high supinator ridge, and distal width with a third articular surface. That of *Perameles* also shows a deflected deltopectoral surface, but the bone is even stouter, the supinator ridge less high and a supratrochlear foramen is present.

An interesting feature in the humerus of *Pucadelphys* is the great development of the areas for the extensors of the forearm and the carpus, although it is relatively no greater than in terrestrial didelphids such as *Monodelphis* or *Metachirus*. To be noted is the difference between the humeri of these last two forms, both terrestrial, but with some saltatorial capabilities in *Metachirus*.

Ulna - Radius. — The ulna and radius of *Henkelotherium* are slightly longer than the humerus; the proportions are not clear in *Pucadelphys* since the distal epiphyses of these two bones are not preserved, but they appear to have been subequal; the two elements are about equal in *Didelphis* and *Metachirus*. In *Henkelotherium*, the ulna and radius were more slender and closely appressed over the whole length; another notable difference is the stronger olecranon and the deeper sigmoid incisure than in *Pucadelphys*. In *Barunlestes* the two bones have proximally an anteroposterior position relative to each other, a position more typical of metatherians than of eutherians. The olecranon is "slightly bent forwards" (KIELAN-JAWOROWSKA, 1978) like in *Pucadelphys*, but it is shorter, notched anteriorly and terminated by a tubercle; the beak of the olecranon is extended internally in a lip which is absent in *Pucadelphys*.

In *Metachirus* the ulna is more gracile and the olecranon shorter than in *Pucadelphys*, and there is an even more developed upper internal lip above the greater sigmoid cavity, as in *Barunlestes*; also the lesser sigmoid cavity is more distinct and hollow. The same remark concerning the upper lip applies to *Didelphis*; on the contrary, in *Monodelphis* the internal lip is reduced: it thus seems that, contrary to OSGOOD's statement, there is no relationship between the presence of an internal articular surface on the distal extremity of the humerus (present in *Monodelphis*) and the presence of an internal upper lip on the ulna; the latter may also correspond to an extension of the surface for the digit flexor muscles. In *Monodelphis*, the bone is again more gracile than in *Pucadelphys*, but the olecranon is as high and the morphology very similar. The olecranon is particularly high in *Philander*, but the bone is rather stout.

In *Barunlestes*, the proximal surface of the radius is much more complex than in *Pucadelphys*, this time in a eutherian fashion. In *Metachirus*, *Monodelphis* and *Didelphis*, this surface is similar to that of *Pucadelphys* but more rounded. In the latter, the diameter of the radius relative to that of the ulna comes closer to that of *Metachirus* and *Monodelphis* than to *Didelphis*, but the bones are relatively more stout.

In *Metachirus* and *Didelphis*, the ulna and radius remain slightly apart for the whole length in the latter and for the upper third in the former, *Metachirus* being thus closer in this respect to *Pucadelphys*. The two bones remain somewhat more apart in *Monodelphis*, the radius being more curved. *Perameles* is very specialized in this area and not comparable to the other forms examined here.

In conclusion, the general stoutness of the ulna and radius in *Pucadelphys* can be considered as primitive, and no particular morphological specialization distinguishes these bones from those of living terrestrial didelphids.

PELVIC GIRDLE (Figs 31A, 41, 42 and 47B; Table 13).

Three elements: 6106, complete, ventral view; 6110, left ilium (all views) and ischium (external view) - part of right ilium and ischium (internal view); 6111, nearly complete, left and right ilium and ischium, dorsal view.

The suture between the ilium and ischium is clear dorsally, that between the ischium and pubis clear ventrally, but that between ilium and pubis is less distinct.

Ilium. —The ilium forms a little more than half the length of the pelvis, which makes it relatively short; its main characteristics are the strong anterior eversion, the thinness and the dorsoventral expansion of the anterior part. It is an elongated, spatula-shaped bone, with a deep dorsoventral iliac wing, and a long but not so deep iliac body. The iliac wing flares anterolaterally; the dorsal border is acute, the ventral border even more so and the iliac crest which unites them anteriorly is rounded and thin. The lateral (gluteal) surface is concave laterally in the longitudinal direction; more laterally and dorsoventrally, the wing is divided by an oblique crest into a concave lateroventral (iliac) surface (Fig. 42, i s) and a convex lateral surface. The internal surface is uniformly concave for vertebral muscles (anterior half) and for the sacral rib more distally (auricular half); the entire iliac wing remains thin.

The much thicker iliac body is narrower dorsoventrally, but flares somewhat distally in front of the acetabulum (a c); its ventral (iliac) face (i f) is well delimited and rounded. The dorsolateral face is slightly concave, and the endopelvic face deeply concave. The dorsal border joins the iliac wing by a deep notch, the great sciatic (g s n). Details of the acetabulum are not observable, the cavity being filled in all cases with the femoral head; the majority of the cavity is ischiatic.

Ischium.— The ischium is nearly as long as the ilium, extending posteriorly from the ilium as a thick longitudinal branch which flattens distally. In dorsal view this branch is twisted, the medial border becoming dorsolateral (long sciatic spine (s s) plus weakly concave sciatic notch) and at the same time the medial face becomes dorsal. The ventral face of the same branch is slightly convex immediately behind the acetabulum and the cotyloid notch; it becomes flat posteriorly on

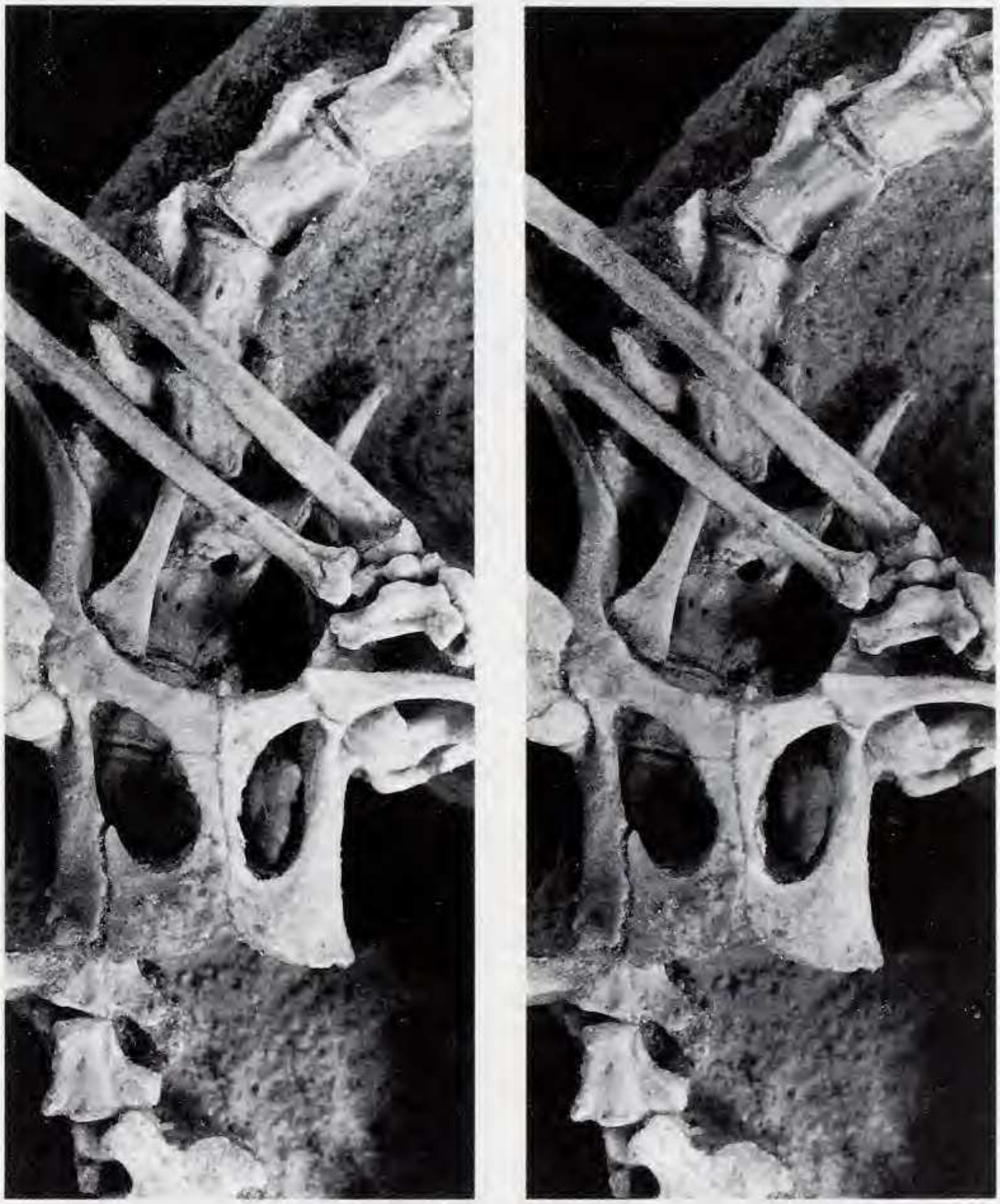


FIG. 41. — *Pucadelphys andinus*. Stereophotos. 6106, pelvis and L3-C6, ventral view; right tibia, fibula and tarsus, external view. X 3.

FIG. 41. — Pucadelphys andinus. *Stéréophotos. 6106, pelvis et L3-C6, vue ventrale; tibia, péroné et tarse droits, vue externe. X 3.*

both sides; the distal branch is wide and flat and makes a right angle with the longitudinal branch. The ischiatic participation to the symphysis is not known since the suture between pubis and ischium is not visible at that level. The ischiatic tuberosity (i t) is little pronounced. There is no obturator tubercle.

Pubis. — The two branches of the pubis make an obtuse angle one with the other; the acetabular branch is relatively narrow and the longitudinal branch even narrower. There is only a weak pectineus tubercle (p t) at the ilio-pubic junction. The obturator foramen (o f) is obliquely elongated and the pubic symphysis (s) relatively long. There is no pubic tubercle at the anterior junction of the two pubes.

Os marsupium.—The os marsupium (nearly complete left and right in 6106; proximal part of right in 6111) is a long, thin, flat and relatively short bone that is broad basally, where it occupies only about 40% of the anterior pubic border; it tapers proximally and bends slightly laterally (Fig. 41; Table 14).

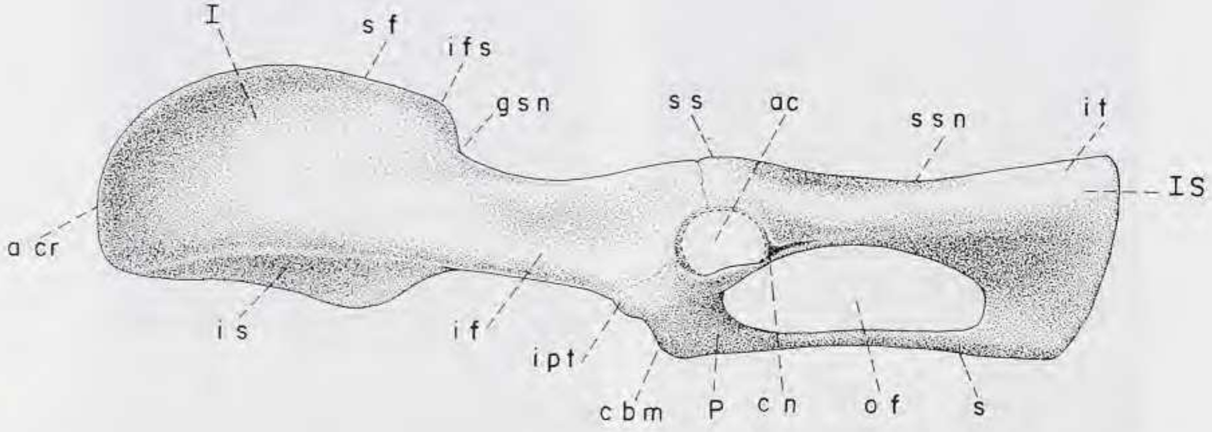
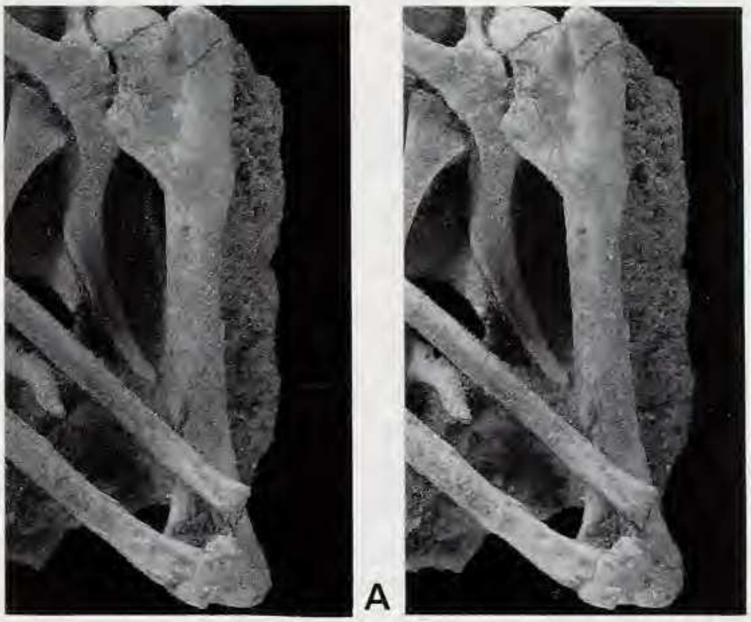


Fig. 42. — *Pucadelphys andinus.* 6106 and 6111 combined, left lateral face of pelvis, restored. X 5. Abbreviations: **I**, ilium; **IS**, ischium; **P**, pubes. **ac**, acetabulum; **a cr**, anterior crest; **c b m**, contact border for os marsupium; **c n**, cotyloid notch; **g s n**, great sciatic notch; **i f**, iliac face; **i f s**, inferior posterior spine; **i s**, iliac surface; **i t**, ischiatic tuberosity; **o f**, obturator foramen; **s**, symphysis; **s f**, sacral face; **s s**, sciatic spine; **s s n**, small sciatic notch.

Fig. 42. — Pucadelphys andinus. *Face latérale gauche du bassin (reconstruction basée sur 6106 et 6111). X 5. Abréviations:* ***I****, ilion;* ***IS****, ichion;* ***P****, pubis;* ***ac****, acetabulum;* ***a cr****, crête antérieure;* ***c b m****, bord de contact pour l'os marsupial;* ***c n****, incisure cotyloïde;* ***g s n****, grande incisure sciatique;* ***i f****, face iliaque;* ***i f s****, épine inférieure postérieure;* ***i s****, surface iliaque;* ***i t****, tubérosité ischiatique;* ***o f****, foramen obturateur;* ***s****, symphyse;* ***s f****, face sacrée;* ***s s****, épine sciatique;* ***s s n****, petite incisure sciatique.*

Fig. 43. — *Pucadelphys andinus.* Stereophotos. A, 6106, right femur, posterior view; partial tibia and fibula, external view, X 3; B, 6105, left femur, tibia and fibula, external view. X 3.

Fig. 43. — Pucadelphys andinus. *Stéréophotos. A, 6106, fémur droit, vue postérieure; tibia et péronés, vue externe. X 3; B, 6105, fémur gauche, tibia et péroné, vue externe. X 3.*


A


B

HINDLIMB

Femur (Figs 43, 44, 45C and 47A; Table 15). — Seven elements: 6105, left, missing proximal end, anterior and external views; 6106, complete left, posteroexternal view - complete right, posterior view; 6110, complete right, posterior and both lateral views - complete left, anterior and partly posterior views; 6111, complete left, anterior, posterior and external views - complete right, anterior and external views.

The femur is slightly longer than the humerus; it is practically straight, and greatly expanded proximally.

The head (Fig. 44, h) is wide, hemispherical, and its base is circumscribed by a suture line. A very shallow fovea capitis for the ligamentum teres is visible, in an excentric position. The neck is very short, making an angle of 40° with the diaphysis. The greater trochanter (g t) is slightly bent anterointernally; it does not reach the level of the top of the head but only that of its sutural base; it is broad and borders externally the deep trochanteric fossa (t f); a marked and short ridge delimits the latter externally; but no clear intertrochanteric ridge delimits it internally, only a marked bump (tc c). The lesser trochanter (l t) is particularly large, lamellar and V-shaped with the apex directed internally; a notch joins it with the base of the head. The third trochanter (t t) is represented by a modest swelling on the external face of the diaphysis situated across from the distal edge of the lesser trochanter.

On the anterior face, the bone is extremely concave under the crest of the greater trochanter, then convex except for a sulcus along the edge of the external border. Further down, the diaphysis is ovoid in cross-section, with an anterior flattening.

On the distal end, the condyles protrude posteriorly as usual; the external condyle (e c) is wider transversely and the internal condyle (i c) longer anteroposteriorly; but they reach about the same level distally. Anteriorly, the patellar fossa is high, wide and shallow. The external trochlear crest is slightly sharper than the internal one. The susepicondylar tubercles (s c t) are modest but distinct.

Patella. — There is no evidence of an ossified patella.

Tibia (Figs 41, 43, 45, 46, 47A and 48; Table 16). — Six elements: 6105, complete left, external view; 6106, complete right, external view - complete left (except for small part of diaphysis), internal view; 6110, proximal half of left, external view; 6111, left, external view - right, posterior view.

The tibia is slightly longer than the femur. The diaphysis is nearly straight (at least as preserved), although in anterior view the tibial crest has a slight sigmoidal curve. On the proximal surface, the interarticular spine is higher than the two lateral articular facets, of which the external one (Fig. 46, e f) is the larger. The anterior, external and internal tuberosities are not very prominent; a distinct fibular facet (f f) occurs on the posteroexternal surface, just below the external articular facet which overlaps the shaft. Proximally, the diaphysis is triangular in cross section (apex anterior), while distally it is flattened externointernally, but it remains relatively wide anteroposteriorly. The external surface is flat proximally, then transversely concave distally; the internal surface, barely convex proximally, becomes flat distally. Posteriorly and proximally,

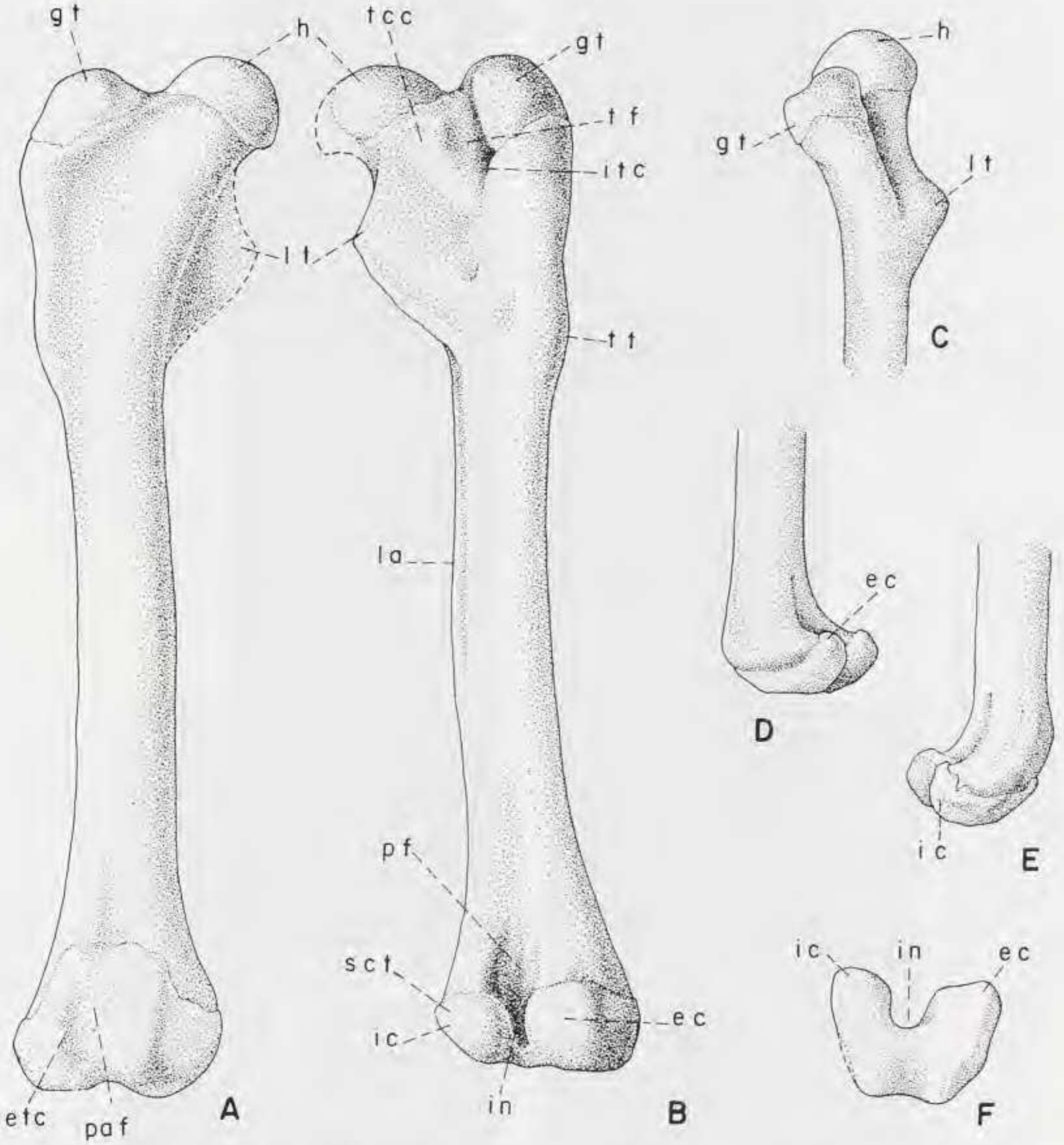
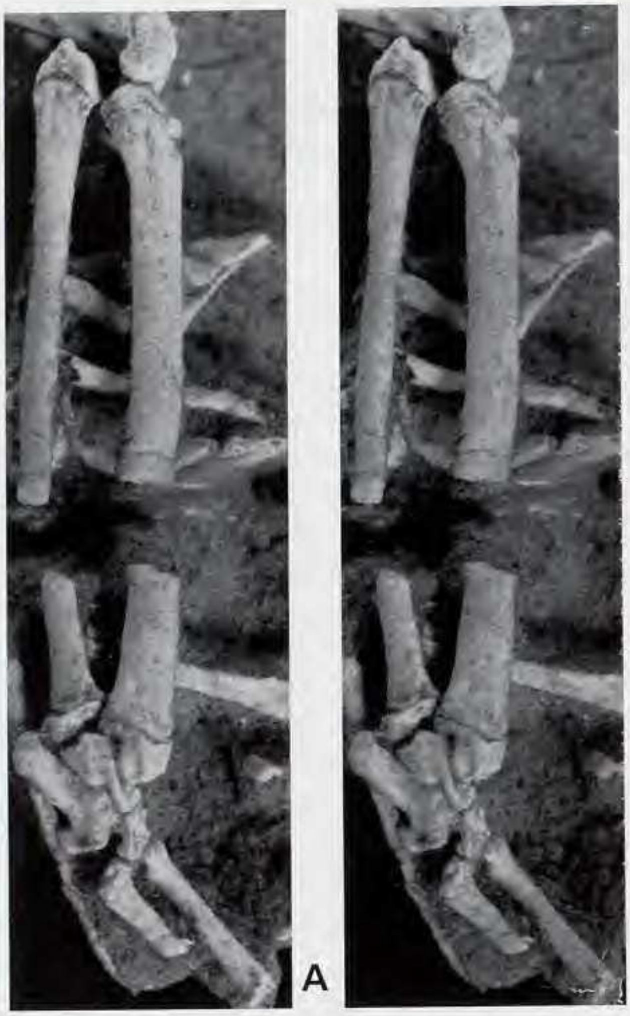


FIG. 44. — *Pucadelphys andinus*. Femur, partly restored: A, anterior face of right (combined left and right 6106 and 6110); B, posterior face of right (combined left and right 6106 and 6110); C, external face of right proximal end (6110+6111); D, external face of left distal end (left 6111 and right 6110 reversed); E, 6110, distal surface of right; F, 6106, internal view of left distal end. X 5. Abbreviations: **e c**, external condyle; **e t c**, external trochanteric crest; **g t**, greater trochanter; **h**, head; **i c**, internal condyle; **i n**, intercondylar notch; **i t c**, intertrochanteric crest; **l a**, ligne âpre; **l t**, lesser trochanter; **p f**, popliteal fossa; **pa f**, patellar fossa; **s c t**, sus-condylar tubercle; **t c c**, bump (voir texte); **t f**, trochanteric fossa; **t t**, third trochanter.

FIG. 44. — Pucadelphys andinus. *Fémur partiellement restauré: A, face antérieure du fémur droit (reconstitution basée sur 6106 et 6110); B, face postérieure du fémur droit (basée sur 6106 et 6110); C, face externe de l'extrémité proximale droite (basée sur 6110 et 6111); D, face externe de l'extrémité distale gauche (basée sur le spécimen 6111 gauche et le spécimen 6110 droit renversé); E, 6110, surface distale du fémur droit; F, 6106, vue interne de l'extrémité distale gauche. X 5. Abréviations:* ***e c****, condyle externe;* ***e t c****, crête trochantérienne externe;* ***g t****, grand trochanter;* ***h****, tête;* ***i c****, condyle interne;* ***i n****; échancrure intercondylienne;* ***i t c****, crête intertrochantérienne;* ***l a****, ligne âpre;* ***l t****, petit trochanter;* ***p f****, fosse poplitée;* ***pa f****, fosse patellaire;* ***s c t****, tubercule sus-condylien;* ***t c c****, bosse (voir texte);* ***t f****, fosse trochantérienne;* ***t t****, troisième trochanter.*


A


B

there is a wide and deep vertical depression; a faint "ligne oblique", which separates the popliteal surface from that for the flexor digitorum, continues to the mid-length of the bone. Distally, the bone widens somewhat; the internal malleolus (i m) projects slightly more distally than the external malleolus (e m) of the fibula. The distal articular surface itself is not accessible.

Fibula (Figs 41, 43, 45, 46A, 47A and 48; Table 17). — Six elements: 6105, complete left (except for distal epiphysis), posterior and external views; 6106, complete right, posteroexternal view - left, anteroexternal view; 6110, proximal half of left, external view; 6111, greater part of left, anterointernal view - nearly complete right (lacking only distal epiphysis), internal view.

The fibula is slightly shorter and more slender than the tibia. The two bones are completely separated. The fibula flattens somewhat proximally and distally, while remaining relatively robust at mid-length; at that level, it is semi-circular in cross-section. Proximally the styloid apophysis (Fig. 46, s a) is prominent; a distinct tibial facet occurs on the internal face making a salient lip, and the bone is strongly concave posteroexternally for a short distance. At the distal end, there is a broad internal facet for the astragalus (a f) and the external malleolus (e m) is well developed.

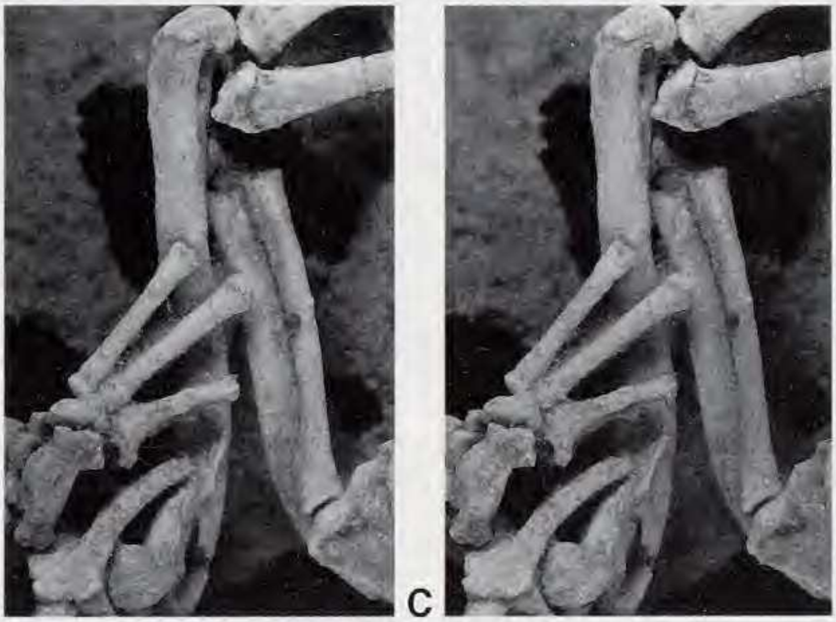


FIG. 45. — *Pucadelphys andinus*. Stereophotos. A, 6106, left tibia and fibula, tarsals and two metatarsals, internal view. X 3; B, 6105, left tibia and fibula, lateral view. X 3; C, 6106, left femur, proximal part of tibia and fibula (top), internal view; ulna and radius (bottom), anterior view, and right foot, dorsal view. X 3.

FIG. 45. — Pucadelphys andinus. *Stéréophotos. A, 6106, tibia et péroné gauches, tarsiens et deux métatarsiens, vue interne. X 3; B, 6105, tibia et péroné gauches, vue latérale. X 3; C, 6106, fémur gauche, partie proximale du tibia et du péroné (en haut), en vue interne; cubitus et radius (en bas), en vue antérieure, et pied droit, en vue dorsale. X 3.*

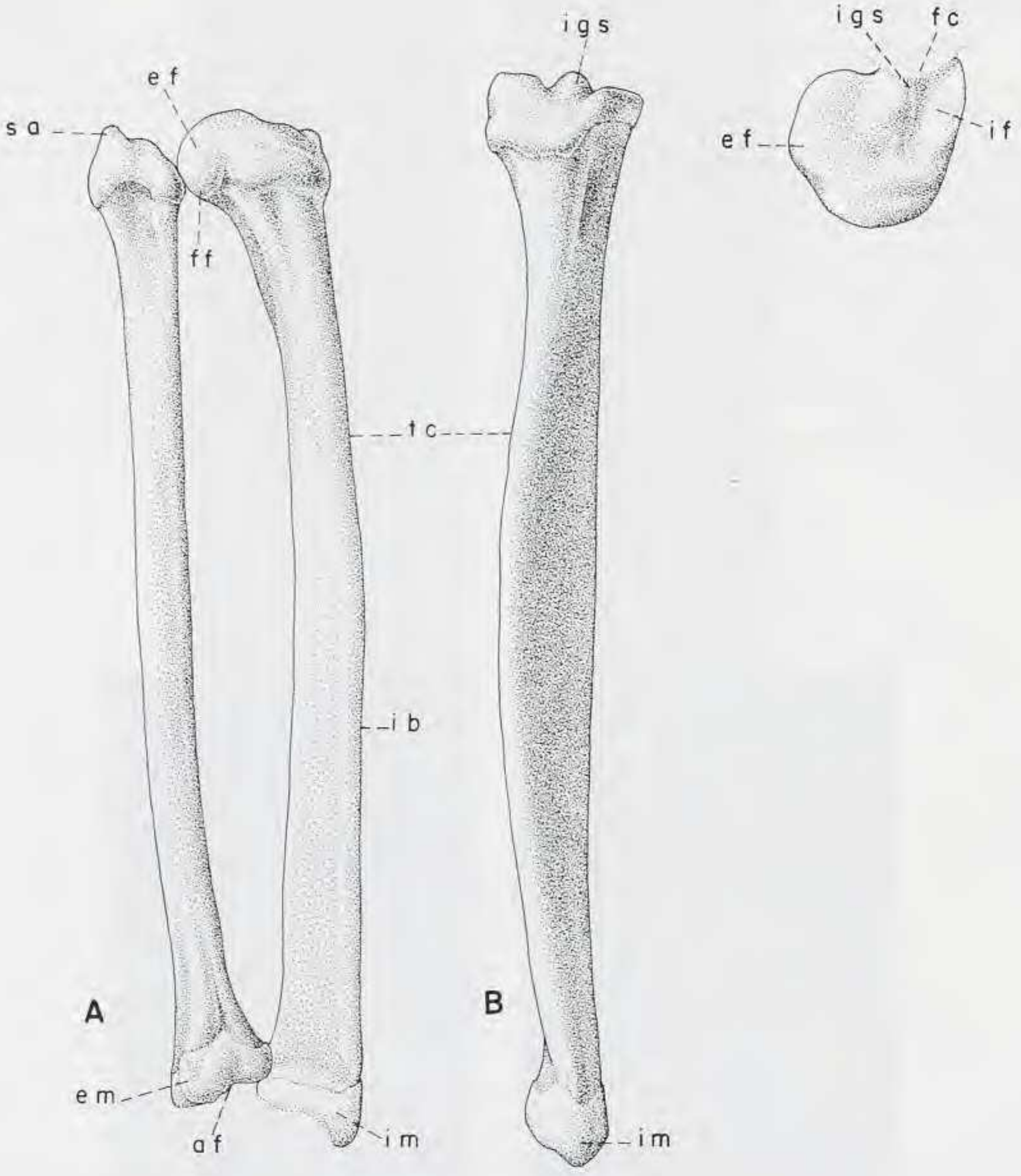


FIG. 46. — *Pucadelphys andinus.* A, 6106, right tibia and fibula, anteroexternal face; B, 6106, right tibia, anterior face; C, 6106, right proximal surface. X 5. All drawn as preserved. Abbreviations: **a f**, astragalar facet; **e f**, external facet; **e m**, external malleolus; **f c**, femoral condyle; **f f**, fibular facet; **i b**, interosseous border; **i f**, internal facet; **i g s**, interglenoid spine; **i m**, internal malleolus; **s a**, styloid apophysis; **t c**, tibial crest.

FIG. 46. — Pucadelphys andinus. *A, 6106, tibia et fibula droits, face antéro-externe; B, 6106, tibia droit, face antérieure; C, 6106, tibia droit, surface proximale. X 5. Dessins en l'état de conservation. Abréviations:* ***a f****, facette astragalienne;* ***e f****, facette externe;* ***e m****, malléole externe;* ***f c****, condyle fémoral;* ***f f****, facette fibulaire;* ***i b****, bord interosseux;* ***i f****, facette interne;* ***i g s****, épine interglénoïde;* ***i m****, malléole interne;* ***s a****, apophyse styloïde;* ***t c****, crête tibiale.*

Pes

Elements of the pes that include some tarsals and associated metatarsals are represented on the left and right sides of 6106. Reference of these elements to the pes is certain because the tarsals remain articulated with the tibia and fibula. Two other element groupings (6105 left, 6110 left) are also cautiously assigned to the pes because of their possible relationships with tibia and fibula, although in these cases they are not directly articulated with these bones. The elements common to these two last groupings are indistinguishable, but the ?cuboids of 6110 are not identical to those of 6106 and the ?metatarsals of 6105 are generally shorter and more robust than in 6106. We attribute these differences to individual variation, but because the cuboid of the pes and unciform of the manus are very similar in didelphids, we are unable to state decisively that the elements in 6105 and 6110 are not, in fact, of the manus.

Astragalus (Figs 41, 45A and C, and 48). — Three elements: 6106, left, dorsal view—right, partial ventral view; 6111, left, ventroposterior view. All three specimens are displaced and squeezed between the distal ends of the tibia and fibula on one hand, and the calcaneum on the other, and thus are distorted and give only partial views of the bone.

It appears that no neck separated the "head" from the "body": the former is only partly visible. Dorsally, a continuous ridge (the medial trochlear crest) separates the inner malleolar facet (Fig. 48, i m f), deep and elongated, from the tibial or trochlear facet (t f); the latter is shallow. A ridge essentially parallel to the first but weaker and shorter (the lateral trochlear crest) isolates a concave fibular facet (f f) on the external side of the astragalus. For the plantar face, and if one interprets correctly 6111, the concave surface corresponding to the calcaneum (CaA of Szalay, 1982) is high and narrow, and limited distally by a condyle; a wide interosseus sulcus separates the CaA from the distal condyle, where the surfaces for the sustentaculum tali, and for the navicular more distally, are practically continuous one with the other.

Calcaneum (Figs 41, 45A and C, 48, 49, 50 and 51; Table 18). — Five elements: 6105, complete left, isolated, all views; 6106, nearly complete right, external view - nearly complete left, ventral view; 6110, nearly complete right, isolated, all views; 6111, incomplete left, external view.

The following description is based on 6105 left (Fig. 49). The posterior half or heel accounts for almost 50% of the total length of the calcaneum; it curves internally at the posterior end. It is high dorsoventrally and narrow from side-to-side; the dorsal border is even narrower than the ventral one. It terminates with a robust tuber calcanei (t c), the posterior face of which slopes anteroventrally; the medial side is more bulbous than the lateral. The anterior half of the calcaneum is subequal in length and breadth. The dorsal surface is dominated by a high, ovale tuberosity for one of the two calcaneo-astragalar facets (CaA); medial to it is a broad shelf, the sustentaculum tali (s t), supporting the small and ill-defined second calcaneo-astragalar facet; close to the CaA is the narrow, anteroposteriorly elongate sulcus calcanei (s c), pierced by a tiny vascular foramen. The long axis of the CaA is oblique relative to the axis of the heel (~45°); its surface itself is convex, more so on the external side, and no clear fibular surface (CaFi) is discernible (unless the external border of this facet is for the fibula?). Anterior to the CaA is a notable expansion, the distal process

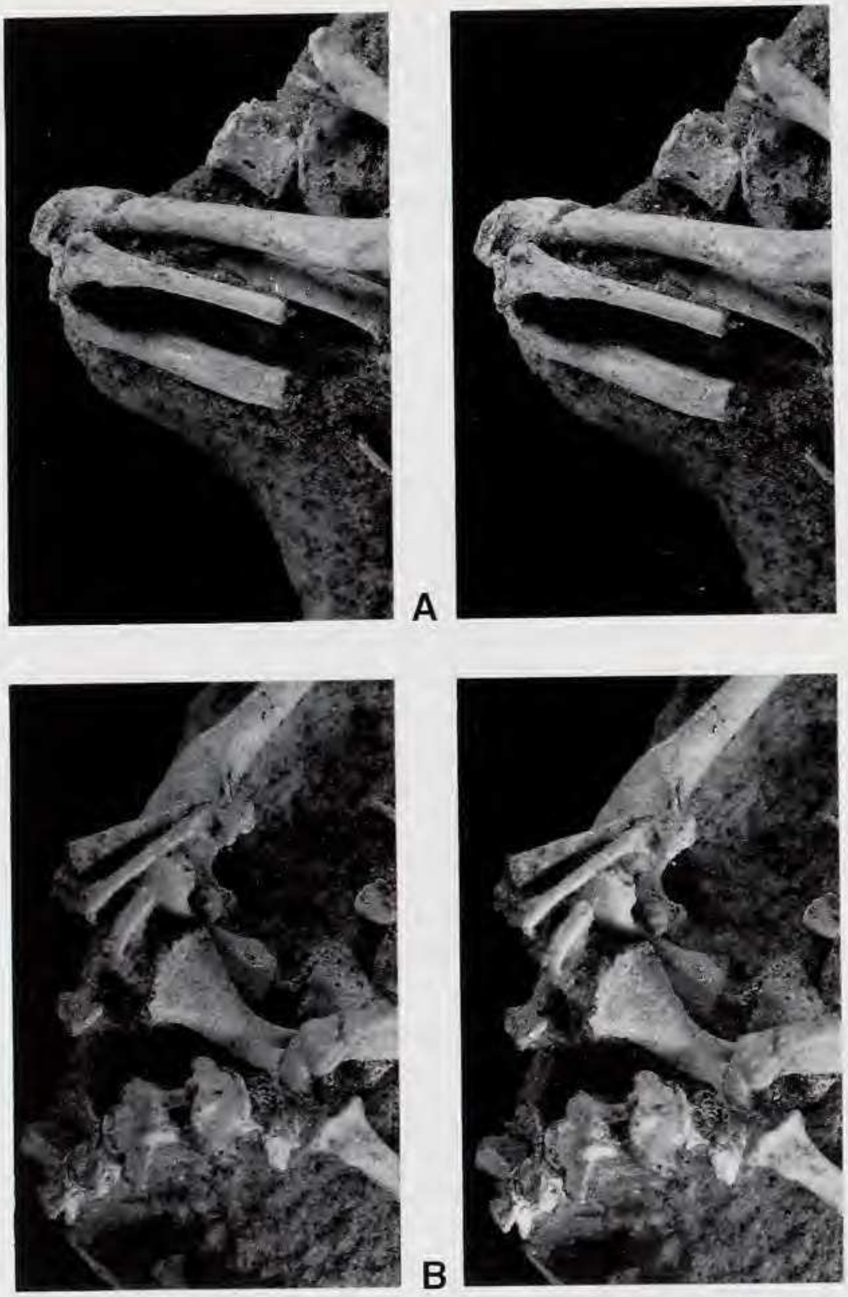


FIG. 47. —*Pucadelphys andinus.* Stereophotos. A, 6110, right femur, external view; half tibia and fibula and last thoracic vertebra, ventral view. X 3; B, 6110, proximal part of left femur, left ischium, right cuboid and metatarsals II, III, IV, dorsal view. X 3.

FIG. 47. — Pucadelphys andinus. *Stéréophotos. A, 6110, fémur droit, vue externe; demi-tibia et péroné et dernières vertèbres thoraciques, vue ventrale. X 3; B, 6110, partie proximale du fémur gauche, de l'ischion gauche, du cuboïde droit et des métatarsiens II, III, IV, vue dorsale. X 3.*

(d p), which is slightly convex dorsally, a convexity limited internally by a strong concavity, but the sulcus for the tendon of the peroneus brevis is poorly defined (gt pb). The concavity is limited externally by a rounded rim corresponding to a well developed peroneus process (p p) (somewhat incomplete on the specimen). The edge of the distal and peroneal processes limit dorsally the cuboidal facet (c f).

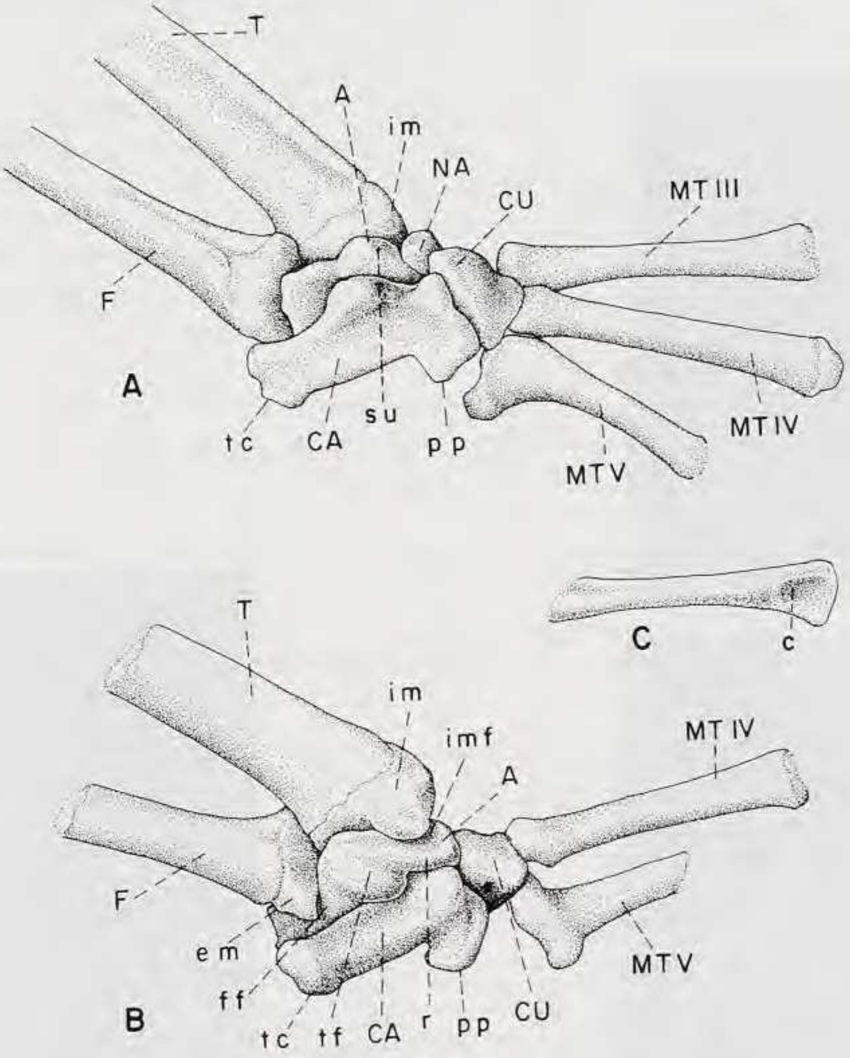


FIG. 48. — *Pucadelphys andinus*. A, 6106, right pes, dorsal face; B, 6106, left pes, ventrolateral face; C, 6110, left metatarsal III, proximal extremity, external face. X 5. Drawn as preserved. Abbreviations: **A**, astragalus; **CA**, calcaneum; **CU**, cuboid; **F**, fibula; **MT**, metatarsal; **NA**, navicular; **T**, tibia; **c**, cavity for adjacent metatarsal; **e m**, external malleolus; **f f**, fibular facet; **i m**, internal malleolus; **i m f**, inner malleolar facet; **p p**, peroneal process; **r**, ridge, see text; **su**, sustentacular condyle; **t f**, trochlear facet.

FIG. 48. — Pucadelphys andinus. *A, 6106, pied droit, face dorsale; B, 6106, pied gauche, face ventro-latérale; C, 6110, métatarsien III gauche, extrémité proximale, face externe. X 5. Dessins en l'état de conservation. Abréviations:* ***A****, astragale;* ***CA****, calcanéum;* ***CU****, cuboïde;* ***F****, péroné;* ***MT****, métatarsien;* ***NA****, naviculaire;* ***T****, tibia;* ***c****, cavité destinée au métatarsien adjacent;* ***e m****, malléole externe;* ***f f****, facette fibulaire;* ***i m****, malléole interne;* ***i m f****, facette malléolaire interne;* ***p p****, processus péronéen;* ***r****, côte, voir texte;* ***su****, condyle sustentaculaire;* ***t f****, facette trochléaire.*

In plantar (ventral) view, the peroneal process forms a triangular point anteriorly; it is quite protruding and is bordered internally by a bump (b), the distal plantar tubercle; between the two is a groove, presumably for the digit V abductor. The cuboidal facet is vaguely diamond-shaped and quite shallow; it is inclined from anterior to posterior and external to internal, and nearly perpendicular to the long axis of the bone.

The calcaneum 6110 is smaller than 6105, as is the entire specimen; it is also somewhat abraded. Its main difference concerns the cuboidal facet, which is oriented more internally than distally.

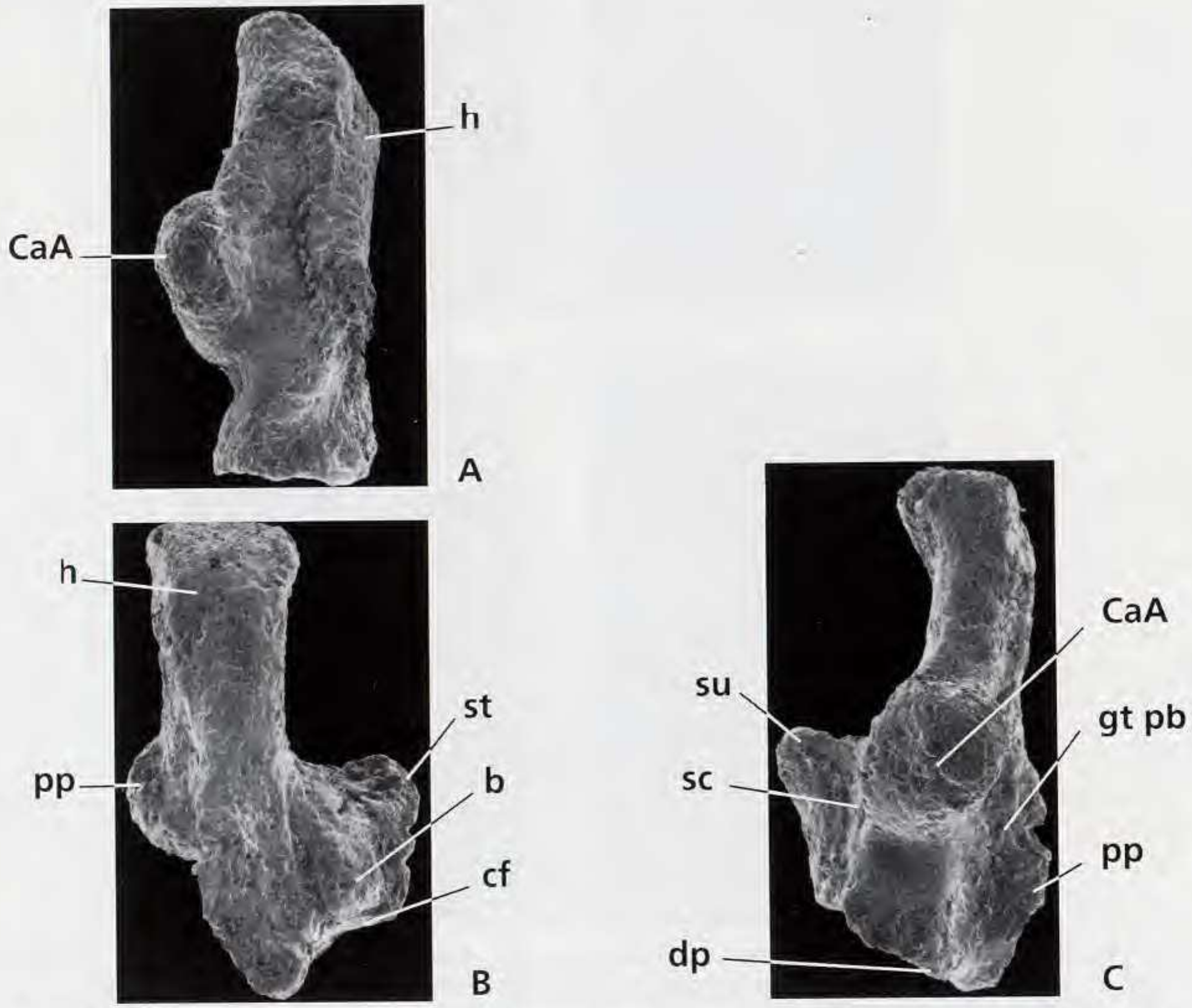


FIG. 49.— *Pucadelphys andinus*. 6105, left calcaneum: A, external face; B, ventral face; C, dorsal face. X 15. Abbreviations: **b**, bump (see text); **CaA**, astragalar condyle; **c f**, cuboidal facet; **d p**, distolateral process; **gt pb**, groove for tendon of peroneus brevis; **h**, heel; **p p**, peroneal process; **s c**, sulcus calcanei; **s t**, sustentaculum tali; **t c**, tuber calcanei.

FIG. 49.— Pucadelphys andinus. *6105, calcanéum gauche: A, face externe; B, face ventrale; C, face dorsale. X 15. Abréviations:* ***b**; bosse (voir texte);* ***CaA**, condyle astragalien;* ***c f**, facette cuboïdienne;* ***d p**, processus disto-latéral;* ***gt pb**, sillon pour le tendon du peroneus brevis;* ***h**, talon;* ***p p**, processus péronéen;* ***s c**, sulcus calcanei;* ***s t**, sustentaculum tali;* ***t c**, tuber calcanei.*

Navicular (Figs 4, 41, 45C and 48). — One element: 6106, right, complete but partly hidden by adjacent bones.

Cuboid (Figs 45A and C, 48 and 52; Table 19). — Two certain elements: 6106, right, dorsal view—left, plantar view. Two uncertain elements: 6110 right, all views except ventral; and 6105 left, dorsal and external views.

The cuboids of 6106 show a triangular dorsal face (Fig. 52C), with a distal base articulating with the whole surface of metatarsal IV and a small part of metatarsal V (su IV-V). This dorsal face is almost flat; its internal border is slightly indented for the cuneiform. Proximally a crest separates the internal and external surfaces: the former is deep, flat and quadrangular. The external face (Fig. 52B), articulated for more than the proximal half with the calcaneum (c s), and dorsally with the navicular (n s) seems to be almost flat; the distal half of this external face bears two tuberculae separated by a deep pit for the tendon of the peroneus longus muscle (t p l). Finally, the ventral face seems to be narrow and convex from side-to-side.

The cuboid? of 6110 differs essentially in its proportions, being stouter, and also in the calcanear facet, which is clearly convex proximodistally. The dorsoexternal bump is much more protruding than the ventral one. These differences may be attributed to better preservation of the bone in 6110. On the distal face, the facet for metatarsals IV and V forms a broad triangle; no relief delimitates the respective facets for these two metatarsals; however, that for metatarsal V must have been very narrow. A very small astragalar facet is discernible on the proximal corner.

Cuneiform IV? (Figs 5 and 52A, C; Table 19). — One element: 6110, left, dorsal and internal views.

It is transversely narrow, short, concave and recurved mesially for contact with cuneiform III, convex laterally for the cuboid. It seems to bear a proximal bump ventrally.

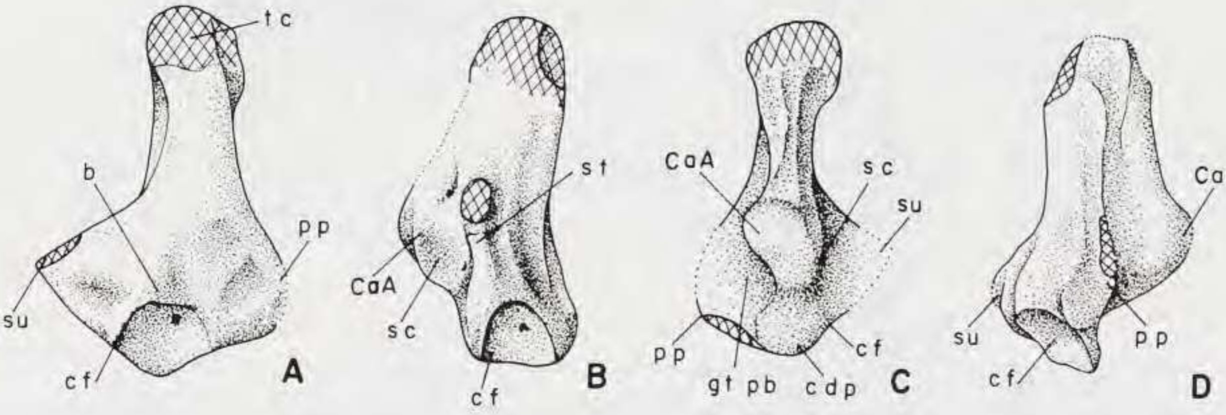


FIG. 50. — *Pucadelphys andinus*. 6110, right calcaneum: A, plantar view; B, internal view; C, dorsal view; D, external view. X 9. Drawn as preserved. Abbreviations: see caption to Fig. 49.

FIG. 50. — Pucadelphys andinus. *6110, calcanéum droit: A, vue plantaire; B, vue interne; C, vue dorsale; D, vue externe. X 9. Dessins en l'état de conservation. Abréviations: voir légende Fig. 49.*

Metatarsals (Figs 4B, 33B, 45A and C, 47B and 48; Table 20). — Represented in four specimens: 6105?, left, II-V, dorsal view; 6106, right, III-V, dorsal view - left, IV and proximal half of V, dorsal view; 6110?, left, II, III and distal part of IV, dorsal view.

As mentioned above, the relative robustness of the left metapodials of 6105 compared to the undisputable metatarsals of 6106 (though of lesser amplitude than the discrepancy observed between the foot and hand of *Didelphis*) led us to suspect the reference of these metapodials to the manus rather than pes. Nevertheless, we cautiously choose to interpret this difference as individual variation.

In length, the middle metatarsals (II, III, IV) are about one third the length of the tibia-fibula; metatarsals III and IV are subequal in length, II is slightly shorter and V is the shortest. On II to IV, the distal end is broader than the proximal; V differs in having, proximally, a broad laterally directed flange (extending well beyond the cuboidal articulation) while its distal end is narrower. The shape of these distal ends is similar for III and IV; but on II the mesial side is expanded and on V the lateral side is expanded; this end is strongly convex with a deflection on each side, and a depression dorsally and ventrally. On II to IV the diaphysis is subrounded in cross-section at mid-

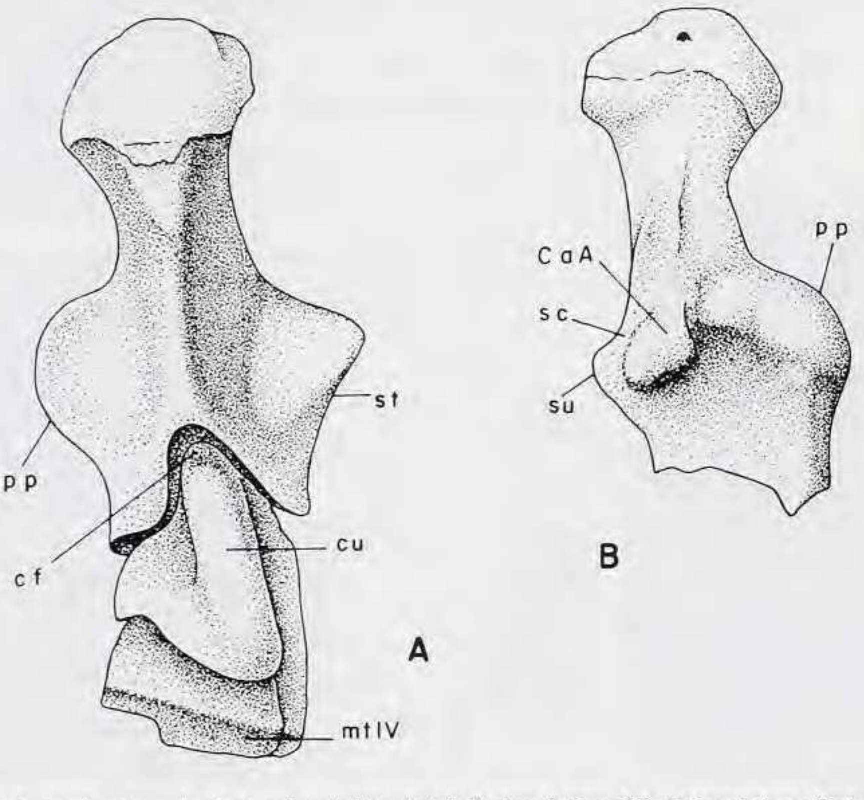


FIG. 51. — *Didelphis*. Left calcaneum: A, plantar view (with cuboid); B, dorsal view. X 3. Abbreviations: **CaA**, astragalar condyle; **cu**, cuboid process; **mtIV**, surface for metatarsal IV; **p p**, peroneal process; **s c**, sulcus calcanei; **st**, sustentaculum tali.

FIG. 51. — Didelphis. *Calcanéum gauche: A, vue plantaire (avec cuboïde); B, vue dorsale. X 3. Abréviations:* ***CaA****, condyle astragalien;* ***cu****, processus cuboïdien;* ***mtIV****, surface pour le métatarsien IV;* ***p p****, processus péronéen;* ***s c****, sulcus calcanei;* ***st****, sustentaculum tali.*

length. Internally and proximally each metatarsal is encased in a pit of the previous one (Fig. 48C, c), thus making the pes a rather rigid unit. This arrangement and preservation of the digits II to V suggest that digit I was, at least, partly divergent, hence possibly opposable.

Phalanges (Fig. 33B). — One proximal phalange in 6105 (left). It is about half the length of the metatarsals. The proximal extremity is wider than the distal, which is convex with no lateral deflection; only a pit borders this convexity on each side.

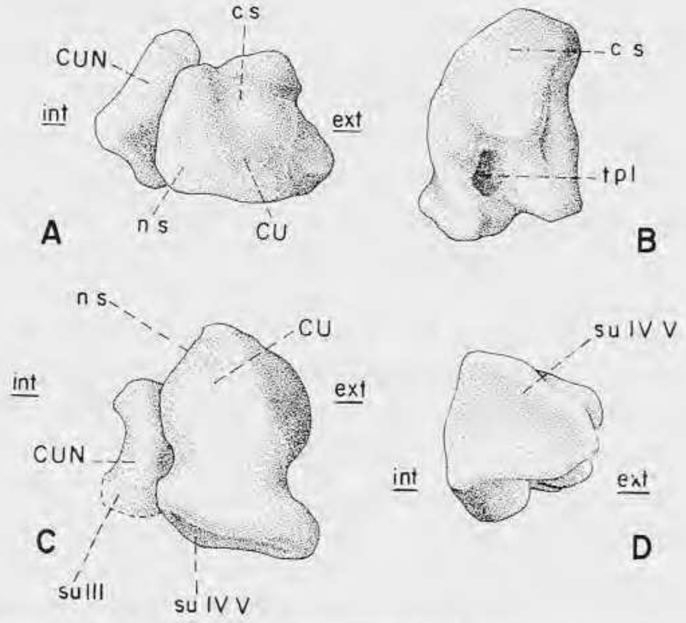


FIG. 52. — *Pucadelphys andinus*. 6110, left ?cuboid and ?cuneiform IV: A, proximal face of both; B, external face of ?cuboid; C, dorsal face of both; D, distal face of ?cuboid. X 9. All drawn as preserved. Abbreviations: **c s**, calcanear surface; **CU**, cuboid; **CUN**, cuneiform; **ext**, external; **int**, internal; **n s**, navicular surface; **suIII**, surface for metatarsal III; **suIV**, surface for metatarsals IV-V; **t p l**, pit for tendon of peroneus longus.

FIG. 52. — Pucadelphys andinus. *6110, ?cuboïde et ?cunéiforme IV gauches: A, face proximale des deux os; B, face externe du ?cuboïde; C, surface dorsale des deux os; D, face distale du ?cuboïde. X 9. Dessins en l'état de conservation. Abréviations:* ***c s****, surface calcanéenne;* ***CU****, cuboïde;* ***CUN****, cunéiforme;* ***ext****, externe;* ***int****, interne;* ***n s****, surface naviculaire;* ***suIII****, surface pour le métatarsien III;* ***suIV****, surface pour les métatarsiens IV-V;* ***t p l****, fosse pour le tendon du peroneus longus.*

DISCUSSION

Pelvis. — In *Henkelotherium,* the pelvis is very similar to that of *Pucadelphys,* with an elongate ilium and symphysis, a clear incisura acetabuli, and a small participation of the pubis to the acetabulum; however, in *Henkelotherium*, the ilium is relatively longer, apparently not as deep and somewhat thicker, and no posterior iliac spine is developed. The ischium is more robust distally, the obturator foramen relatively smaller, and the stout os marsupium occupies the whole anterior border of the pubis; there is no ilio-pectineus tubercle, which we interpret as the primitive state.

In *Barunlestes*, the main differences with *Pucadelphys* concern the iliac wing, which is relatively longer and narrower, and the wider obturator foramen; the ilio-pectineus tubercle is developed as well as a sciatic spine. There may have been an os marsupium in that genus, as suggested by the presence of a concavity on the anterior margin of the pubis (KIELAN-JAWOROWSKA, 1975).

In *Metachirus*, the ilium is not as everted as in *Pucadelphys*; it is also relatively longer, with a thickened anterior border and a not so deep ventral wing. But the ischium and pubis are very similar to those of *Pucadelphys*, with a similar limitation of the os marsupium to the medial half of the anterior border of the pubis, and an open symphysis angle. *Perameles* also resembles *Pucadelphys* in the high, thin, everted iliac wing, though it is relatively longer; but the ventral face of the ilium is wider, and there is practically no incisure in the acetabulum; the os marsupium is narrower than in *Pucadelphys*, being reduced to a rod; the distal ischiatic branch is also wider, hence the obturator foramen is smaller and the ventral puboischiatic carina is not salient. This carina is, on the contrary, very salient in *Monodelphis*, where the ilium is longer relative to the ischio-pubic part than in *Pucadelphys* and thicker than in *Metachirus*. Finally, the pelvis of *Didelphis* is more different, with a much longer and thicker ilium; the lateral ridge is very thick and the ventral face is ventroexternal; it has a relatively longer sacral surface for the two sacral vertebrae; the os marsupium is much wider distally. The pelvis of *Philander* is close to that of *Didelphis*, with a lower ilium and a short puboischium, but the very short os marsupium occupies only half of the anterior pubic border. The sutures between the three pelvic components are clear only in the subadult specimen of *Metachirus* used for comparison.

We conclude that *Pucadelphys* has a peramelid-like ilium, the dorsoventral anterior expansion of which we regard as a specialization, as well as the large size of the obturator foramen and the smallness of the os marsupium. But the relative shortness of the ilium and the massiveness of the ischio-pubic ensemble conform to what we infer to be the primitive state.

Femur. — In *Henkelotherium*, the femur is very similar to that of *Pucadelphys*; but the angle between the head and diaphysis is only 30° and there is no third trochanter. *Barunlestes* shows more differences: angle 60°, neck longer, greater trochanter higher, lesser trochanter less expanded proximodistally but more internally, internal condyle larger.

The femur of *Metachirus* is, as the humerus, more slender than that of *Pucadelphys*, with also a longer neck; the tuberosity internal to the trochanteric fossa is much more prominent, the greater trochanter reaches higher and there is hardly any third trochanter (the latter is said to be rare in marsupials: only three genera are mentioned by OSGOOD, 1921); finally, the slope of the distal border is quite steep, the medial condyle extending distally beyond that of the lateral condyle. The same remarks apply to *Didelphis*, where these features are more accentuated. The femur of *Philander* is robust and particularly wide distally; the neck and lesser trochanter are well developed, and the greater trochanter reaches the top of the head. The femur of *Monodelphis* resembles that of *Pucadelphys* in its proportions, its low greater trochanter and the quasi-absence of a neck, but the intertrochanteric fossa is less deep, the lesser trochanter is not so well developed though of the same shape and there is no third trochanter, no more than in *Perameles*; in this genus the lesser trochanter is even more reduced, and shows again some specializations, particularly distally, that are probably related to fossorial adaptations. The fovea capitis occupies the same position in *Pucadelphys* and *Metachirus*, but it is better delimited and deeper in the latter; it is also faint in *Monodelphis* and poorly delimited, but situated higher on the head; it is eccentric in *Eozostrodon* too, less so in *Didelphis* and *Perameles*, but clearly circular.

Overall, the femur of *Pucadelphys* appears somewhat more generalized than those of the living didelphids.

Tibia-Fibula. — From the figurations, the tibia of *Henkelotherium* seems to have been more curved than in *Pucadelphys*; in any case this is true of *Metachirus*, where the bone narrows more in the distal half. But in the latter genus, the general morphology is very close to that of *Pucadelphys*, including details of the proximal surface and those of the internal face of the internal malleolus. One difference concerns the medial proximal facet, which is narrower, longer and deeper; these characters are even more accentuated in *Didelphis* and *Perameles*. The tibia of *Monodelphis* is also sigmoidal, narrower anteroposteriorly, but otherwise again very similar to that of *Pucadelphys*.

In *Barunlestes* the tibia and fibula are partly fused (an apomorphy found in some eutherians), and the tibia is more curved and narrower distally than in *Pucadelphys*.

In *Henkelotherium*, the fibula remains quite thick as in *Pucadelphys*. In *Metachirus* (and *Monodelphis*) the fibula is at the same time much more slender and more expanded proximally, and the tibial articular surface is less salient medially and distally. The specialisations toward fossorial adaptations observed on the femur of *Perameles* apply to the tibia-fibula. In all didelphids the two bones are completely and widely separated.

The fibula of *Pucadelphys* is clearly not as specialized as in living didelphids, being intermediate between those of the latter and that of *Henkelotherium*.

Astragalus. — The astragalus of *Pucadelphys* differs from that of *Didelphis*, where a short neck separates head and body: the condition in *Pucadelphys*, also present in *Caenolestes*, is considered to be primitive by OSGOOD (1921). The configuration of the two tibial facets suggests that the tibia of *Pucadelphys* was well locked with the astragalus so as to allow only slight lateral movements. Moreover, in *Didelphis* the CaA is more crescent-like, the interosseous relatively narrower and the condyle for the sustentaculum tali is more distinct. Dorsally the trochlear is even shallower but wider.

Only a very partial astragalus is preserved in *Henkelotherium*. That of *Barunlestes* is very different, with a distinct neck, and a medial ridge shorter than the lateral ridge. The astragalus of *Deccanolestes*, a placental from the late Cretaceous of India, is of interest in our comparisons because it has been shown by GODINOT & PRASAD (1994) to display arboreal specializations, in the trochlea (lateral crest higher than the medial crest, a condition opposite to that of *Pucadelphys*), in the angulation of the navicular facet relative to the sustentacular facet (again contrary to the situation of *Pucadelphys*).

Calcaneum. — The preserved part of the calcaneum of *Henkelotherium* is reduced to the tuber calcis. That of *Zalambdalestes* lacks a peroneal tubercle and the cuboidal facet is perpendicular to the long axis of the bone, both states being more derived than those of *Pucadelphys*. In *Didelphis* (Fig. 51), the calcaneum has a relatively shorter heel, the sustentacular facet is clearly delimited (not in *Pucadelphys*) but there is no deep sulcus between it and the CaA; the long axis of the CaA (which is relatively less salient) is not so oblique relative to that of the heel. An important specialization of the calcaneum of didelphids is the plantar indentation which extends the cuboidal facet, itself completely terminal; the distoventral orientation of the cuboidal facet in *Pucadelphys* would thus seem to foreshadow the didelphid state.

The calcaneum of *Pucadelphys* is thus different from that of Szalay's "metatherian morphotype" (1982a and b); in particular, the apparent absence of a fibular facet (CaFi, Szalay, 1982) corresponds rather to his "didelphid morphotype tarsus", with a bicontact upper ankle joint (UAJ); however, this calcaneum resembles the plesiomorphic metatherian morphotype in having a large peroneal process and "remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum" (Szalay, 1982a: 626). The presence of a large peroneal process is also mentioned in *Deccanolestes* (Prasad & Godinot, 1994) but is there interpreted as "related to powerful movements of inversion and eversion", hence to a very mobile foot; this character is indeed associated, in this genus, with other indicators of such a condition, for instance: difference in the size of the astragalar and calcanear caA, well rounded astragalar navicular facet.

Cuboid. — The cuboid of *Didelphis* is indented distally, and the articular surface for metatarsal V is better delimited. The greatest difference occurs ventrally, with the development of the proximal longitudinal process directed towards the secondary facet on the calcaneum. The intermeshing of cuboid and cuneiform III occurs in *Didelphis* and also in *Philander*.

Pes. — No tarsus of *Metachirus*, *Philander* or *Monodelphis* was available for comparison. The pes of *Perameles* is very specialized for digging, with a narrow tarsus and metatarsus.

In *Henkelotherium*, the metatarsals represent about 1/3 of the length of the tibia-fibula. In *Monodelphis*, the metatarsals equal less than 1/4 the length of tibia-fibula and the digits are interlocked proximally as in *Pucadelphys*. In *Philander*, the metatarsals are short (1/6th the length of tibia-fibula) and not linked to one another; II>III =IV>V. In *Didelphis*, the metatarsals, independent from one another, are only 1/5th the length of the tibia-fibula; III>II =IV>V.

Thus, the foot of *Pucadelphys* (where the metatarsals represent more than 1/3 the length of the tibia-fibula) was relatively long and rigid.

The proximal phalanges are almost as long as the metatarsals in *Henkelotherium* and *Philander*, slightly more than half as long in *Monodelphis* and *Didelphis* (and about half in *Pucadelphys*).

HABITS

About 22 species of mammals are known from Tiupampa, of which 50% are eutherian and 50% metatherian. As demonstrated by all skeletal and dental remains thus far collected, *Pucadelphys andinus* is the most abundant species of mammal in this fauna (Marshall & Muizon, 1988).

Based on the adult specimens (6105 and 6106), *Pucadelphys andinus* measured about 135 mm from tip of snout to base of tail, and about 270 mm from tip of snout to tip of tail (assuming the presence of ±30 caudal vertebrae). In size it compares with some living species of *Marmosa* and with *Lestodelphis halli* (MARSHALL, 1977), and thus weighed about 50 grams.

LOCOMOTION. — Many living didelphids are terrestrial (*e.g. Lutreolina, Lestodelphis, Metachirus, Monodelphis*, some *Marmosa*) and those that have arboreal capabilities (*e.g.* some *Marmosa, Philander, Didelphis*) are often found on the ground. *Perameles* is specialized for digging and lives in burrows. From the above description, what can be deduced about the locomotion in *Pucadelphys*?

HILDEBRAND (1961) concluded from his study of body proportions in didelphids that the measurements of the various long bones did not yield any significant results: "the more arboreal animals differ from the semi-arboreal and terrestrial animals in behavior patterns but not in morphology". Also, JENKINS (1971) insisted justly on the importance of physiological factors in locomotion : "even if biomechanical conditions are similar, there may be profound differences .. in, for example, agility, in ratio or intensity of locomotor activity"; and in 1974, the same author noted: "the differences between arboreality and terrestriality of tree shrews is at times only behavioral". Finally, BARNETT & NAPIER (1953) wrote that "there is remarkably little morphologic difference between the form and mobility of the fibula in the ecologically distinct species (arboreal, unspecialized terrestrial and aquatic)". However, GRAND (1983) remarked that, whereas *Metachirus and Monodelphis* are both terrestrial, the hindlimb elongation in the former genus coincides with its agility and bounding locomotion; *Monodelphis*, with his subequal anterior and posterior limbs, remains effectively slower.

Before proposing locomotion capabilities of *Pucadelphys*, we shall summarize its skeletal characteristics:

1. Short spinous processes of the cervicals, are compatible with good flexibility of the neck.
2. Large dorsal metapophyses, long lumbar spinous processes as well as broad distal end of humerus are suggestive of digging abilities, while the same long and widely distant lumbar spines favor leaping capabilities (SLIJPER, 1946; GAMBARYAN, pers. comm., 1992).
3. The smallness of the space between ulna and radius suggests a very limited rotation of the forearm; the relation between the two bones seems to indicate a slight anteroexternal proximal superposition, a side-by-side position along the diaphyses and a slight anterointernal superposition distally.
4. The pelvis usually reflects locomotory specializations: leaping or digging forms have recognizable features on the bone, but these are extreme cases; for less specialized forms, interpretation is not so clear. Also, the shape of the pelvis not only depends on function but also on its relation to the viscera, as indicated by ELFTMAN (1929). In *Pucadelphys* we have noted a possible mobility of the sacro-iliac joint (as in *Perameles*); the broadness of the sacrum and the large ilio-sacral angle (both as in the digging form *Perameles)*; the wide, flat and laterally flaring surfaces for the erector spinae and gluteus medius (abductor and extensor of the thigh), again as in *Perameles*; similarly the pronounced downward curvature of the transverse processes of lumbar vertebrae corresponds to powerful erector spinae (ELFTMAN, 1929). The propulsive part part of the pelvis (behind the iliac

blade) is short, though not as short as in *Perameles*. The ischia are elongated to provide leverage for the hamstrings and increase the power of the adductors as extensors of the thigh as in leaping or digging forms; measurements for is/il ratio are: *Perameles*, 0.67; *Pucadelphys*, 0.53; *Didelphis*, 0.36; *Metachirus*, 0.47; *Monodelphis*, 0.37. All of these observations suggest digging capabilities for *Pucadelphys*. However, the posterior border of the ischium is slightly inclined forward and downward (while it is more vertical in *Perameles*): this can be interpreted as giving less strength to the extensors; also there is no strong buttress on the acetabulum, anteriorly or posteriorly (such a buttress is strong in digging forms), and finally the iliac muscle (which extends from the ventral surface of the ilium to the smaller trochanter and prevents the body from falling forward when digging) is esteemed to have been modest in *Pucadelphys*. But it should be kept in mind that there are many ways of digging and thus adaptive strategies can be different.
5. Relative limb proportions of *Pucadelphys*, with subequal fore- and hindlimbs, are intermediate between those of *Metachirus* and *Monodelphis*, and testify to a good agility (JULIEN-LAFERRIÈRE, 1991).
6. A tibia locked to the astragalus corresponds to a relatively rigid hindlimb (as opposed to an arboreal form); the relatively strong fibula (as in generalized marsupials: BARNETT & NAPIER, 1953) has only a limited distal contact with the tibia. Finally, the well developed internal and external malleoli usually indicate saltatorial capabilities (BARNETT & NAPIER, 1953)
7. The astragalus and calcaneum of *Pucadelphys* do not show arboreal specializations such as mentioned above (GODINOT & PRASAD, 1994), though the large peroneal process may indicate good mobility. The pes is relatively long, and it is deduced from the preservation of 6106 that the 1st digit (itself missing on the specimen) was at least slightly divergent; if not, one would assume that metatarsal I would have been preserved along with II and III (the big toe is only slightly divergent in *Monodelphis*, more so in *Metachirus*; note that divergence does not necessarily mean opposability, and simple opposability does not mean arboreality). Moreover, the united metapodials suggest a rigid pes: united digits and long metapodes are usually related to digitigrady, but the latter normally accompanies at least a reduction of digit I, a situation unknown in *Pucadelphys*. Finally, the configuration of the tibio-astragalus joint is not known; we thus ignore if it was such as to allow reversal of the foot, as observed by JENKINS & MCLEARN (1984) in some arboreal didelphids.

Based on the above, we prudently infer that *Pucadelphys* was essentially terrestrial, quite agile but neither cursorial nor saltatorial; it appears to have been capable of bounding and also of some digging, these two abilities being less developed than in *Metachirus* and *Perameles* respectively.

WAY OF LIFE. — *Pucadelphys* was probably nocturnal as are most living didelphids, sleeping in a burrow-nest during the day and foraging for food at night. Most living didelphids are solitary except during the breeding season (WALKER, 1964); MCMANUS (1970) stresses the poor social behavior of *Didelphis*. However, it is not uncommon that one individual would share a burrow with a congenere (or even a "foreigner", SHIRER & FITCH, 1970), especially in cold weather (didelphids with their naked ears, tail and paws are ill adapted to cold weather: FITCH & SHIRER,

1970) and also depending on the population density (Crawley ,1973). Yet, there are no records that two males would huddle together (McManus, 1970; Shirer & Fitch, 1970). These observations suggest two interpretations for the specimen-pairs of *Pucadelphys andinus*: 1) they were male-female pairs that bonded for a restricted breeding season; or 2) that they were two females that shared the same burrow. For females of *Didelphis*, Fitch & Shirer (1970) have observed that, "from time to time, two individuals were staying together in the same den simultaneously; on some occasions it seemed that the animals must have been side-by-side and in actual contact". A definitive choice between these two interpretations is not possible, as there are no features in either the skull or skeleton of didelphids which permit secure sexual identification [although in small mammals, females are often larger than males; Wooller *et al.*, 1981; but in *Trichosurus*, males are only 1% larger than females (Crawley , 1973)]. Nevertheless, the occurrence of two specimen-pairs (i.e., a repeated association) of *Pucadelphys* at Tiupampa suggests the most natural and simplistic relationship (i.e. male-female pairs), rendering the first interpretation as most likely.

Ground nests of all of the mentioned didelphids have been found in hollow logs, under rocks or in burrows (Walker, 1964). *Didelphis* curls in a den when it is cool, limbs close to the body, head under body; when very hot it lies on its back (McManus, 1970). Thus, the "died-in-a-burrow" hypothesis (see above), and the three dimensional life-like position of the fossilized specimens are consistent with observed behavior and habits of some living didelphid taxa.

CONCLUSIONS

The vertebrate fauna from Tiupampa accumulated in channels of meandering rivers on a flat alluvial plain. The presence of several groups of crocodiles attests to a warm, probably subtropical climate. The fauna is from the middle member of the Santa Lucía Formation which, based on a detailed magnetostratigraphic study, would be between 59.5 and 59.0 Ma (Sempere *et al.*, in prep.).

The four specimens of *Pucadelphys andinus* described here represent the earliest and most complete articulated skeletons of metatherians yet known. The two sets of what are interpreted to be male-female pairs were found in a three dimensional, life-like, snout-rump position in burrow-nests that were apparently dug in a river bank. The animals probably died as the result of a flood which entrapped them in their burrows and filled the latter with water and sediment. Functional considerations of the skeletons suggest that *Pucadelphys* was essentially terrestrial, quite agile, and possessed limited bounding and digging capabilities. The vast majority of character states in the skeleton of *Pucadelphys* are regarded as mammalian, tribosphenic and metatherian plesiomorphies (i.e. atlas imperforate and with a persisting suture between ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; strong fibula; presence of ossified os marsupium). The plesiomorphic states of the cervical vertebrae are not collectively found in any living didelphid examined.

Numerous other skeletal features of *Pucadelphys* also do not occur as a suite in any of the didelphids examined. These include: 1) a single fulcral vertebra (S2); 2) a long, non-prehensile tail; 3) specialized lumbar series (gradual lengthening of vertebral body and transverse processes, and long anteriorly directed neural spines); 4) specialized pelvis (ilium dorsoventrally expanded anteriorly, large obturator foramen, small os marsupium); 5) possible movable sacro-iliac joint; and 6) digging specializations of the humerus [no third distal articular surface (Osgood, 1921), large areas for extensors of forearm and carpus]. Except for feature 2 and a small os marsupium (part of 4), the others are specializations reflecting the bounding and digging capabilities noted above.

The only postcranial element that reflects the phylogenetic position of *Pucadelphys* within Metatheria is the calcaneum. This bone has a bicontact upper ankle joint (UAJ) which is diagnostic of the family Didelphidae; moreover, the partially plantar orientation of the cuboidal facet can be interpreted as foreshadowing the state in living Didelphidae where the calcaneum has a distinct ventral indentation of the cuboidal facet. The calcaneum of *Pucadelphys* also approaches the "plesiomorphic metatherian morphotype" of Szalay (1982a, b; 1984) in having a large peroneal process and remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum. This combination of tarsal states supports the interpretation based on the study of the skull, dentary and dentition (Marshall & Muizon, this volume) that *Pucadelphys* represents the most plesiomorphic taxon within the family Didelphidae.

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APPENDIX: measurements

In the following tables, all measurements (in mm) are of specimens of *Pucadelphys*. The abbreviation *ca.* is used in the sense of "estimated". But it should be made clear that all measurements are to be taken with caution, the figures obtained depending on the orientation and focus choosen by the operator.

Dans les tableaux suivants, toutes les mesures (en mm) sont celles de Pucadelphys andinus. *L'abréviation* ca *indique qu'il s'agit d'une estimation. Mais toutes ces mesures doivent être considérées avec prudence, les valeurs obtenues dépendant en partie de l'orientation et de la mise au point choisies par l'opérateur.*

TABLE 1. — Measurements of atlas and axis.
TABLEAU 1. — *Mesures de l'atlas et de l'axis.*

specimen		6105	6110
Atlas (CV1):			
	Width of axoidian facet	1.5	1.3
	Mxm length of arch	2.0	2.4
	Ventral length	0.9	1.2
Axis (CV2):			
	Length of neural arch	4.1	4.2
	Mxm length	5.4	4.7
	Height of dens	0.7	0.5
	Width of dens	1.2	1.1
	Height of neural arch	ca. 3.9	ca. 3.9
	Mxm width at atlantal articulation	5.0	4.4
	Width of tv.proc. (dorsal root) as preserved	8.0	
	Posterior width of centrum	2.8	2.4

TABLE 2. — Measurements of cervical vertebrae 3 to 7.
TABLEAU 2. — Mesures des vertèbres cervicales 3 à 7.

specimen			6105
CV 3	Centrum:	Length	2.4
		Anterior width	2.4
		Posterior width	2.6
CV 4	Centrum:	Length	2.0
		Anterior width	2.8
		Posterior width	2.6
CV 5	Centrum:	Length	1.8
CV 6	Centrum:	Length	1.7
CV 7	Centrum:	Length	1.65

TABLE 3. — Measurements of thoracic vertebrae.
TABLEAU 3. — Mesures des vertèbres thoraciques.

specimen			6105	6106	6110	6111
T1	Centrum:	Length	2.3	2.4		
		Anterior width	2.9	1.9		
		Posterior width	2.3	2.0		
	Width of transverse processes		8.4	6.8		
T2	Centrum:	Length	2.4	2.4		
		Anterior width	2.3			
		Posterior width	2.8			
	Width of transverse processes		ca. 5.0			
T3	Centrum:	Length	2.5	2.7		
	Width of transverse processes			ca. 5.0		
T4	Centrum:	Length	2.75	2.7		
T5	Centrum:	Length	2.6	2.9		
T6	Centrum:	Length	2.55	2.8	2.2	
		Anterior width			ca. 1.6	
		Posterior width			ca. 1.8	
T7	Centrum:	Length	2.0	3.0	ca. 2.2	
		Anterior width			ca.1.6	
		Posterior width			ca. 1.7	
T8	Centrum:	Length	2.6	3.0	2.2	
		Anterior width			ca. 2.0	
		Posterior width			ca. 2.0	
T9	Centrum:	Length	ca. 2.8	3.0	2.3	ca. 1.9
		Anterior width			ca. 2.1	
		Posterior width			ca. 2.2	
T10	Centrum:	Length		3.1	2.3	ca. 1.9
T11	Centrum:	Length		3.1	2.4	ca. 2.0
T12	Centrum:	Length		3.2	2.45	2.4
T13	Centrum:	Length		3.6	2.65	2.5

TABLE 4. — Measurements of lumbar vertebrae.
TABLEAU 4. — Mesures des vertèbres lombaires.

specimen			6106	6110	6111
L1	Centrum:	Length	3.7	3.0	2.5
		Anterior width	3.0		2.0
		Posterior width	3.6		ca. 2.4
	Width of transverse processes		4.0		
L2	Centrum:	Length	4.5	3.0	ca. 2.9
		Anterior width	2.9		
		Posterior width	2.8		
	Width of transverse processes		5.0		
L3	Centrum:	Length	4.9	3.8	ca. 3.3
		Anterior width	2.8	4.0	
		Posterior width	3.0		
	Width of transverse processes		5.6		
L4	Centrum:	Length	5.3	3.8	3,3
		Anterior width	2.8		
		Posterior width	3.1		
	Width of transverse processes		6.5		
	Length of spinous process		4.00		
L5	Centrum:	Length	5.0	3.5	3.7
		Anterior width	3.0		
		Posterior width	4.5	3.1	
	Width of transverse processes		6.9		
	Length of spinous process		4.20		
L6	Centrum:	Length	4.3	3.0	ca. 2.9
		Anterior width			
		Posterior width	3.9	2.5	
	Width of transverse processes		8.1		
	Length of spinous process		4.90		

TABLE 5. — Measurements of sacral vertebrae.
TABLEAU 5. — Mesures des vertèbres sacrées.

specimen			6106	6110	6111
S 1 + S 2	Length		7.4	6.5	5.5
S 1	Centrum:	Length	3.4	3.1	ca. 2.5
		Anterior width		2.5	
		Posterior width	3.0	2.3	ca 1.9
	Width of transverse processes between pelves		10.0	8.4	6.6
S 2	Centrum:	Length	4.0	3.4	ca. 2.5
		Anterior width	3.0	ca. 2.3	
		Posterior width	3.0		
	Sacral foramen:		(l)	(r)	
		Length	1.0	1.05	
		Width	1.0	1.0	

TABLE 6a. — Measurements of caudal vertebrae (C1 - C9).
TABLEAU 6a. — Mesures des vertèbres caudales (C1 - C9).

specimen			6106	6110	6111
C 1	Centrum: Length		3.7		ca. 2.3
	Anterior width		2.5		
	Posterior width		2.6		
C 2	Centrum: Length		3.7		ca. 2.3
	Anterior width		2.5	2.2	
	Posterior width		2.7	ca. 2.25	
	Width of transverse processes		ca. 10.0		
C 3	Centrum: Length		3.5		2.8
	Anterior width				
	Posterior width			2.1	
	Width of transverse processes		ca. 9.8	ca. 5.5	
C 4	Centrum: Length		3.5	ca. 2.6	2.5
	Anterior width			1.9	
	Posterior width		3.0	1.7	2.4
	Width of transverse processes		9.0	ca. 6.6	5.6
C 5	Centrum: Length		4.0	ca. 3.5	3.3
	Anterior width		2.4	1.9	1.9
	Posterior width		2.1		2.2
	Width of transverse processes			ca. 5.4	6.0
C 6	Centrum: Length		5.5		4.3
	Anterior width		2.15		2.1
	Posterior width		2.9		2.5
	Width of transverse processes		ca. 7.0		4.4
C 7	Centrum: Length		7.0		5.0
	Anterior width		2.7		2.2
	Posterior width		3.0		2.2
	Width of transverse processes:	anterior	4.1		4.8
		posterior	ca. 6.0		
C 8	Centrum: Length		7.7		6.9
	Anterior width		2.6		2.5
	Posterior width		2.1		2.3
	Width of transverse processes:	anterior	5.8		
		posterior	4.6		
C 9	Centrum: Length		8.0		
	Anterior width		2.4		2.2
	Posterior width		2.3		
	Width of transverse processes:	anterior	4.6		
		posterior	4.0		

TABLE 6b. — Measurements of caudal vertebrae (C16?, C17?, C20?, C21?).
TABLEAU 6b. — Mesures des vertèbres caudales (C16?, C17?, C20?, C21?).

specimen			6110
C 16?	Centrum:	Length	ca. 6.5
		Anterior width	1.9
		Width of transverse processes: anterior	2.9
C 17?	Centrum:	Length	7.0
		Anterior width	1.4
		Posterior width	1.4
C 20?	Centrum:	Length	6.1
		Anterior width	1.4
		Posterior width	1.6
C 21?	Centrum:	Length	6.4
		Anterior width	1.3
		Posterior width	1.2

TABLE 7. — Measurements of scapula.
TABLEAU 7. — Mesures de l'omoplate.

specimen	6105	6106	
	(l)	(l)	(r)
Length	ca. 15.0		ca.18.0
Maximum proximal width		3.8	4.0
Width of glenoid fossa		ca. 2.0	ca. 2.0

TABLE 8. — Measurements of clavicle.
TABLEAU 8. — Mesures de la clavicule.

specimen	6105	6110	
	(l)	(l)	(r)
Length	10.5		
Width of sternal end	2.0	ca. 1.8	
Width of scapular end	1.1		1.2
Median width	0.9	0.8	0.7

TABLE 9. — Measurements of interclavicle.
TABLEAU 9. — Mesures de l'interclavicule.

specimen	6105
Total length	8.9
Length anterior to costal tuberculae	3.1
Length posterior to costal tuberculae	5.0
Width of end cephalic	1.2
caudal	1.4
Width between costal tuberculae	3.7

TABLE 10. — Measurements of humerus.
TABLEAU 10. — Mesures de l'humérus.

specimen	6105	6106	6110	
	(l)	(l)	(l)	(r)
Length	17.5	20.7	ca. 16.3	17.0
Transverse width proximal end				3.8
Ant.-post. width proximal end		3.7	3.75	3.4
Transverse width distal end	6.3	6.0		4.5

TABLE 11. — Measurements of ulna.
TABLEAU 11. — Mesures du cubitus.

specimen	6105	6106	6110	new specimen
	(l)	(l)	(l)	(r)
Length of olecranon + sigmoid cavity			ca. 4.6	5.0
Length of sigmoid cavity		1.9	1.8	2.5
Depth of olecranon at mid-length		1.6	2.1	2.0
Depth of sigmoid cavity at mid-length	1.9	1.9	1.7	1.7

TABLE 12. — Measurements of radius.
TABLEAU 12. — Mesures du radius.

specimen	6105	6110
	(l)	(l)
Length		ca. 14.0
Width of proximal articular surface	1.65	
Minimum width of diaphysis	1.1	

TABLE 13. — Measurements of pelvis.
TABLEAU 13. — Mesures du bassin.

specimen		6106	6110	6111	
		(l)	(l)	(l)	(r)
Length (ant. edge of ilium to post. edge of ischium)		24.0			18.0
Width between iliac wings (ant. width)		17.0			ca. 10.0
Width between lateral edges of ischium (post. width)		13.0			ca. 10.0
Length of pubic symphysis		10.0			ca. 8.0
Length of ilium		ca. 10.0		10.0	ca. 9.0
Length of ischium			ca.8.0	8.8	9.0
Width of post. end of ischium			ca.4.5	4.5	
Obturator foramen	Length	6.8			
	Width	4.2			

TABLE 14. — Measurements of os marsupium.
TABLEAU 14. — Mesures de l'os marsupial.

specimen	6106	
	(l)	(r)
Length	9.3	
Width of contact with pelvis	3.1	3.2

TABLE 15. — Measurements of femur.
TABLEAU 15. — Mesures du fémur.

specimen	6106		6110		6111	
	(l)	(r)	(l)	(r)	(l)	(r)
Length	25.0	24.5	ca. 20.0	21.0	19.3	19.0
Proximal transverse width	5.7	5.8	5.6			4.5
Distal transverse width	ca. 4.4	4.3	4.3	4.0		
Distal ant.-post. width	3.6	3.5	ca.3.6	ca.3.8	3.1	

TABLE 16. — Measurements of tibia.
TABLEAU 16. — Mesures du tibia.

specimen	6105	6106		6110	6111
	(l)	(l)	(r)	(l)	(r)
Length	23.5		26.5		ca. 19.0
Proximal transverse width	3.7		3.8	4.0	
Proximal ant.-post. width	3.3	3.4	3.5	ca. 3.1	
Transverse distal width	3.3	ca. 3.1	ca. 3.1		2.2

TABLE 17. — Measurements of fibula.
TABLEAU 17. — Mesures du péroné.

specimen	6105	6106		6110	6111
	(l)	(l)	(r)	(l)	(l)
Length	ca. 22.5		ca. 24.5		
Proximal transverse width	ca. 3.0	ca. 3.0		2.6	
Proximal ant.-post. width	1.9				
Transverse distal width		2.3	2.4		2.0
Ant.-post. distal width	2.0				1.7

TABLE 18. — Measurements of calcaneum.
TABLEAU 18. — Mesures du calcanéum.

specimen	6106		6110	6111
	(l)	(r)	(r)	(l)
Length	5.3	5.6	4.2	ca. 4.0
Width of tuber	1.5	1.6		
Distal width	4.0			

TABLE 19. — Measurements of tarsals.
TABLEAU 19. — Mesures des tarsiens.

specimen	6105 (l)	6106 (r)	6110 (l)
Cuboid:			
Length (dorsal length)	1.6	2.3	1.6
Distal width	1.65	1.5	1.5
Cuneiform IV:			
Length (dorsal length)			1.0
Distal width			0.6

TABLE 20. — Measurements of metapodials.
TABLEAU 20. — Mesures des métapodes.

specimen	6105 (l)	6106 (r)	6110 (l)
Metapodial II:			
Length	7.0		ca. 6.5
Proximal width	0.9		0.8
Distal width	1.5		ca. 1.25
Metapodial III:			
Length	7.5	ca. 8.0	ca. 7.0
Proximal width	1.1	1.1	0.8
Distal width	1.5	1.4	
Metapodial IV:			
Length	ca. 7.5	8.0	ca 7.0
Proximal width		1.1	
Distal width		1.6	
Metapodial V:			
Length	6.0	6.3	
Proximal width	2.15	2.5	
Distal width	1.2		
Proximal phalanx:	3.4		